

FINAL REPORT

Pines vs. Oaks Revisited: Forest Type Conversion Due to
High-severity Fire in Madrean Woodlands
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List of Abbreviations/Acronyms

NMDS: non-metric multidimensional scaling; GIS: geographic information system; SE: standard error; USFS: United States Forest Service

Keywords

Forest, fire; fire severity; forest type conversion; Madrean pine-oak forest; oak shrubland; rerouting; drought

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Abstract

Fire regimes have shifted drastically across the American Southwest, from frequent surface fires prior to Euro-American settlement, to fire suppression in the 20th century, to the current era of recent, widespread high-severity wildfires. A key management concern across the Southwest is an increasing prevalence of large crown fires, caused by drought and mounting fuel loads, and consequent shifts in forest stand structure and species composition. We sampled vegetation plots repeatedly from before and after the 1994 Rattlesnake and 2011 Horseshoe Two Fires in the Chiricahua Mountains to evaluate the extent to which repeated crown fires have converted Madrean pine-oak forest to oak shrubland in the Sky Islands of Arizona. As proposed, we addressed four central research questions, herein. First, does conversion of Madrean pine-oak to oak shrubland after high-severity fire persist over the long term? Second, Does the resprouting ability of *P. leiophylla* rescue populations of this species in high-severity fire environments relative to other non-sprouting pines? Third, how does pine and oak regeneration vary across the fire severity gradient, and to what extent are these responses mediated by site characteristics, such as physiography? Fourth, to what extent do plant functional traits and tree ecophysiology influence the post-fire regeneration responses of pines and oaks following high-severity fire?

Our results document that drought and area burned have increased in southeastern Arizona in the past two decades. Plant communities shifted significantly from forests that once contained a mixture of both pines and oaks before the wildfires to dominance by oak resprouts, other shrubs, and grasses by 2016, especially where fires burned at high-severity. In those sites, nearly all stems were killed above-ground, but oaks vigorously regenerated via resprouting, with little pine recruitment. These patterns were consistent since the first high-severity wildfire 22 years ago, and for both fire events in the Chiricahuas. In the wake of the more-recent, Horseshoe Two Fire, seedling recruitment declined with increasing fire-severity, but oak resprouting increased. The differential recruitment success of oaks over pines was amplified by their far greater juvenile height and ramets per resprouting genet. Resprouting in *P. leiophylla* after top-kill was low but sufficient to suggest that this behavior may maintain this species in low numbers after high-severity fire. Topography was a significant influence on fire severity and vegetation response: less exposed areas (e.g. in drainages) experienced lower-severity fire and less conversion to oak shrublands, suggesting that these sites provided refugia for pine after high-severity fire. Low post-fire pine recruitment was found in all plots, across all fire severities, suggesting that forest type conversion was driven by both fire and drought in the past two decades. Species-specific differences in plant functional traits explain the differential success of oak regeneration relative to pines. The pronounced sprouting capacity of oaks, a trait found throughout this genus, confers a striking advantage over obligate-seeder or weakly-resprouting pines. Amplifying this advantage, oak also maintain high photosynthetic efficiency and water status relative to pines during the dry season. Surprisingly, fire severity and physiography do not influence these relationships.

Projections call for continued aridity and crown fire in the Southwest, suggesting that Madrean pine-oak forests may be approaching a tipping point that may lead to their transition to more drought-resistant communities dominated by oaks, although alternative trajectories are still possible. Those projections, our results suggest that both fuel management in current pine fire refugia and field trials to test the ecological and practical feasibility for restoring pines to the landscape are critical for maintaining Madrean pine-oak forest structure and function under a projected future hotter and drier climate.

Objectives

Our original proposal set out four questions with associated hypotheses related to recovery of vegetation after large crown fires in the Southwest.

Question 1: Does conversion of Madrean pine-oak to oak shrubland after high-severity fire persist over the long term? Five years after the Rattlesnake fire, resprouts from top-killed oaks had grown prolifically but seedlings for all woody plants were rare ([1]. Nine years post-fire, oak coppices had grown into an incipient canopy and recruits remained uncommon (Barton, unpublished data). The lack of regeneration by seed is likely attributable to both fire severity and historically low precipitation in the years after the fire [2]. Given the success of oaks, the poor response of pines, the closure of the canopy, and continuing long-term drought, we hypothesized that oak shrubland would persist over the long term in these high-severity fire sites. We hypothesized further that plots burned by a second large, high-severity fire (Horseshoe Two, in 2011) would perpetuate the dominance of an oak shrubland.

Question 2: Does resprouting in *P. leiophylla* rescue populations of this species in high-severity fire environments relative to other non-sprouting pines? We've shown that, while most *P. leiophylla* stems are killed in high-severity fire, a low percentage resprout. At five and nine years after the Rattlesnake Fire, these sprouts exhibited vigorous growth and occupied sites with high light availability or had surpassed their oak competitors in height. Given this success, we hypothesized that these sprouts would continue to perform well and would maintain a small population of *P. leiophylla* within the post-fire oak shrubland.

Question 3: How does pine and oak regeneration vary across the fire severity gradient, and to what extent are these responses mediated by site characteristics, such as physiography? Topography can influence fire line intensity across landscapes [3], and drainages often serve as fire refugia for fire-sensitive species [4]. Recent research suggests that fire regimes in drainages are changing, and that historical fire refugia may be disappearing [5], thus restricting the contemporary distribution of species adapted to infrequent or low-severity fire. Our past work suggests a striking impact of fire severity on post-fire succession: low-severity fire favors pines, and oaks recover through resprouting, whereas high-severity fire has the potential to remove pines and favor oaks. We hypothesized, topography would continue to influence long-term tree recruitment, resulting in spatial structuring of post-fire communities, with drier sites dominated by oak shrubland and moister sites continuing to host both pines and oaks.

Question 4: To what extent do plant functional traits and tree ecophysiology influence the long-term post-fire response of vegetation to high-severity fire? Pine-oak vegetation regenerates after fire by seed or basal sprouting. Studies in post-fire shrub systems show that seedlings often experience high mortality during the first seasonal drought following post-fire germination [6]. We also expected the pines and oaks in this study to differ strongly in both leaf traits and ecophysiological responses (see, for example, Kolb and Stone (7)). We hypothesized that differences in tree regeneration strategy and plant functional traits (specifically plant water relations and photosynthetic potential) would explain the post-fire regeneration response of Madrean woodlands to high-intensity fire.

The questions posed above directly addressed task (7) "Re-measurement – long-term fire effects on vegetation and fuels." We proposed to examine the successional trajectories of Madrean evergreen woodlands in response to high-severity fire, and the physiological mechanisms underlying post-fire regeneration trends. Such information is paramount for guiding future vegetation management activities, especially in the face of projected increases in warmth

and aridity [8, 9]. Specifically, we sought to examine spatio-temporal variation in woodland successional response and recovery (or lack thereof) in a Madrean pine-oak woodland after high-severity fire. The long time-interval since the 1994 Rattlesnake Fire and the multiple sampling-intervals following fire provide insights into both the long-term temporal responses of vegetation to high-severity fire and the process of recovery. Moreover, the variety of topographic positions captured by the plots allow an examination of the spatial differences in species responses associated with both topography and soil moisture availability.

We were fortunate to be able to successfully address and answer all four of the questions posed in the original JFSP grant proposal.

Background

Fire regimes in the American Southwest have shifted dramatically over the past two centuries. Prior to Euro-American settlement, frequent lightning-caused, low-intensity surface fire prevailed [10-12]. Starting in the late 19th century, fire exclusion from livestock grazing and then active fire suppression led to a precipitous decline in fire frequency [13-15]. More than a century of mounting fuel loads from fire exclusion, coupled with an increasingly warmer and drier climate have sparked a recent surge in large, high-severity crown fires throughout the region [16-21]. Like the fire-suppression era before it, this new fire regime is well outside the historic range of variation [*sensu* 22] for most forest types in the American Southwest. Given future projections of both continued high fuel loads and increased aridity, the prevalence of these high-severity fires is unlikely to abate [8, 9].

The rise of large crown fires is causing major shifts in forest stand structure and species composition throughout the Southwest. Forest type-conversions from pine-dominated forest to oak shrublands and grasslands have been well-documented after a spate of high-severity fires in the past two decades [23-26]. Savage and Mast (27) identified persistent non-forested sites decades after stand-replacing fires in *Pinus ponderosa* Lawson & C. Lawson in Arizona and New Mexico, suggesting that these conversions might well be permanent alternative stable vegetation states [28]. Such forest type-transformation is a key forest management concern across the region, and comprehensive assessment of the patterns and underlying mechanisms of these shifts are desperately needed for implementing science-based adaptive management activities in the wake of high-severity wildfire [12, 25, 29].

Most prior forest type-conversion research from high-severity fires in the American Southwest has focused on ponderosa pine forest [e. g., 17, 30, 31], one of the most widespread forest types in the region. We know much less about high-severity fire impacts on other vegetation complexes, such as the Madrean pine-oak forests of the U.S. borderlands and northern Mexico. Madrean evergreen communities in this region represent a global hotspot of biodiversity and endemism [32-35]. While the core of the Sierra Madre lies in Mexico, mountain island archipelagos spill over into the U.S. in the so-called “Sky Islands” of Northern Mexico, southern Arizona, New Mexico, and West Texas. Conversion of these mixed evergreen forests to oak communities after high-severity fire has been documented in Mexico [36] and Arizona [1]. Given their high conservation value, understanding the vegetation responses of these systems to an altered fire regime, and an increasingly hotter and drier climate is of paramount importance.

Arizona Sky Island pine-oak forest is composed mainly of the pines, *Pinus leiophylla* Schiede & Deppe and *P. engelmannii* Carrière, and the sclerophyllous oaks, *Q. arizonica* Sarg., *Quercus emoryi* Torr., and *Q. hypoleucoides* A. Camus. Like *P. ponderosa* forests, these woodlands experienced a frequent surface-fire regime before Euro-American settlement [10, 37-

39]. Pines and oaks differ markedly in their responses to fire [36, 40], where the thick bark and self-pruning of pines historically-conferred a high level of survival under the pre-settlement low-severity, surface-fire regime. In contrast, oaks are readily top-killed, but resprout prolifically in response to a wide range of fire intensities. The exception to this dichotomy is *P. leiophylla*, which, unlike most other pines, exhibits thick bark, self-pruning, and a modest capacity to resprout after fire-induced top-kill [40-42].

In high-severity burn portions of the >11,000 ha Rattlesnake Fire (1994) in the Chiricahua Mountains, most trees were top-killed, all *Quercus* species sprouted vigorously, *P. leiophylla* sprouted at low levels, and few seedlings of any species established up to five years after the fire [1]. Whereas centuries of frequent surface fires had maintained a mix of pines and oaks, high-severity fire transformed Madrean pine-oak forest to oak shrublands. In 2011, the Horseshoe Two Fire burned most of the Chiricahua Mountains (>90,000 ha), > 40% at moderate and high severity, including large areas of Madrean pine-oak forest. Such “megafires” swept the Southwest during 2011, one of the driest on record. The predominance of such large fires in recent years raises the potential of widespread forest type-conversion of Madrean pine-oak forest and a decline of pines [29]. However, little is known about the dynamics and repeatability of these transitions across time and space.

The questions addressed in this project are critical to the management of pine-oak woodlands on federal public lands in the Sky Islands – high value habitats in terms of biological diversity and recreation. Our study tested the hypothesis that continued high-severity fire has the potential to degrade these rich pine-oak habitats in terms of structural and biological diversity. The American Southwest is projected to transition to an even more arid climate (Seager et al. 2007, Williams et al. 2014), and large severe crown fires are likely to persist. The results of our proposed work contribute to an emerging ecological foundation for projecting the fate of Madrean pine-oak forests, especially if society chooses not to adopt adaptation or mitigation strategies for ameliorating the effects of future climatic change.

Materials and Methods

Study System

This study was carried out in the Chiricahua Mountains (Figure 1) in southeastern Arizona (31°52' N, 109°15' W), which form part of the Sky Islands, a northern extension of the Sierra Madre Occidental [43]. The mountains extend southeast to northwest for about 80 km and rise from about 1100 to 3000 m altitude (a.s.l.). Part of the Basin and Range Geological Province, the terrain is rugged and highly-dissected, rising from broad flat basins to rocky uplands, separated by steep-walled canyons. Soils are shallow, mostly derived from volcanic rhyolites and monzonites deposited in the early- to mid- Miocene, although pre-Tertiary rock is prominent at lower elevations [44].

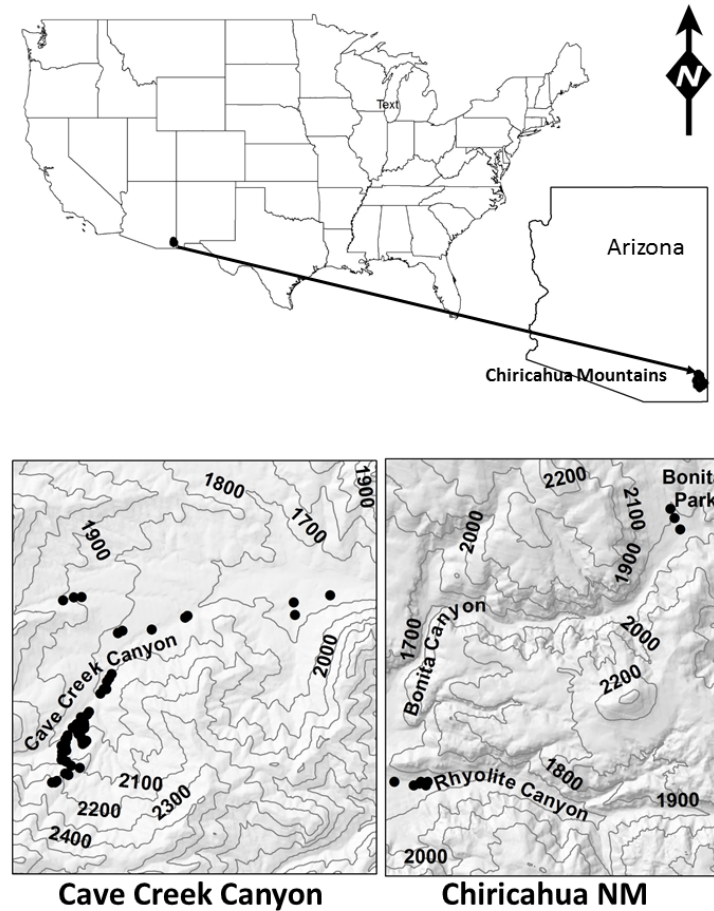


Figure 1: Location map for the Chiricahua Mountains, Arizona, with topographic maps showing the locations of plots in Cave Creek Canyon (Chiricahua National Forest) and Chiricahua National Monument. Three plots along the lower Snowshed Trail are not shown.

The climate is semiarid, with two wet seasons, one between July and September, when more than 50% of total precipitation falls, and the second between December and March. A pronounced dry season usually occurs between the final winter storms in March or April and the onset of the North American Monsoon System in early July [45]. January average minimum and maximum temperatures are -0.2°C and 14.7°C , respectively; July average minimum and maximum temperatures are 17.4 and 32.8°C , respectively. Mean annual rainfall at the Southwestern Research Station (1650 m a.s.l.), near the main study area, is 506 mm.

The research was carried out in Madrean pine-oak forest between 1665 and 2132 m a.s.l, mainly in Cave Creek Canyon on the east side of the Chiricahua Mountains, in Coronado National Forest, but also in Chiricahua National Monument on the west side (Figure 1). Plot locations were selected either to resample permanent geo-referenced plots or to add new ones to ensure capture of the range of variation in both fire-severity and topography.

Before Euro-American settlement (1870s), lightning-caused, surface fires occurred frequently in Madrean pine-oak forests in the Chiricahua Mountains, with a mean fire return interval of 4.2 to 17.9 years, and stand-replacing fires were rare [11, 38, 46]. Fire was uncommon from the 1880s through the 1980s, initially in response to intensive livestock grazing and then active fire suppression [13]. The first contemporary, large, high-severity fire in the Chiricahua

Mountains was the 11,110-ha Rattlesnake Fire (RS) in 1994 [47], in which 21% burned at high severity and 12% at moderate severity (dNBR data; Monitoring Trends in Burn Severity (MTBS) 2012). During the extremely dry year of 2011 [9], the Horseshoe Two Fire (HT) burned >90,000-ha, about 75% of the mountain range, 12.4% at high severity and 29.7% at moderate [48]. The HT fire re-burned nearly all of the area subject to the RS fire.

The Chiricahua Mountains support a wide array of species and communities. Multiple ecoregions converge here, which, combined with steep, highly dissected terrain, promotes vertical stacking of biotic communities over short geographical distances, a phenomenon that occurs across the Sky Island ranges [33-35, 49-54]. From low to high elevations, typical vegetation is characterized by desert scrub and grassland, open piñon-oak-juniper woodland, chaparral, pine-oak forest, gallery forest, Arizona and ponderosa pine forest (*Pinus arizonica* Engelm. and *P. ponderosa*), montane mixed conifer forest, and subalpine spruce-fir forest.

Madrean pine-oak forest is composed primarily of *Pinus engelmannii*, *Pinus leiophylla*, *Q. arizonica*, *Q. emoryi*, and *Q. hypoleucoides*. Other tree life forms include *Arbutus arizonica* A. Gray, *Hesperocyparis arizonica* Greene, *Juniperus deppeana* Steud., *Pinus arizonica*, *Pinus discolor* D.K. Bailey & Hawksw, *Platanus wrightii* S. Watson, and *Pseudotsuga menziesii* Mirb. The shrub layer is variable in cover and includes *Agave palmeri* Engelm., *Arctostaphylos pungens* Kunth, *Ceanothus fendleri* A. Gray, *Cercocarpus montanus* Raf., *Dasyllirion wheeleri* S. Watson, *Garrya wrightii* Torr., *Mimosa aculeaticarpa* var. *biuncifera* Benth., *Nolina microcarpa* S. Watson, *Opuntia chlorotica* Engelmann & J. M. Bigelow, *Quercus rugosa* Nee, *Rhamnus betulaefolia* Greene, *Rhus trilobata* Nutt., *Robinia neomexicana* A. Gray, and *Yucca madrensis* Gentry. Nomenclature follows the USDA Plants Database [55].

Climate and Fire Patterns in Southeastern Arizona

We assessed temporal patterns of moisture availability in southeastern Arizona using historical growing season (June-August) Palmer Drought Severity Index (PDSI) data [1895-2015; 56] to compare moisture availability for the post-RS period (1994-2015) to the rest of the time series (1895-1993). We carried out a similar comparison for fire activity, using the number of fires and area burned for each year from 1921 to 2016 from the Coronado National Forest Fire Atlas [57]. PDSI and fire activity data were modeled using generalized least squares models using the *gl*s function of the *nlme* package [58] in R [59].

Plot Sampling Design

Data for this paper came from a series of inventories initiated in 1988, before large crown fires were common in the Sky Islands, continuing in 1999, 2003, 2008, and culminating in 2016, five years after the 2011 HT Fire and 22 years after the 1994 RS Fire (Table 1, Figure 1). Although most samples were taken from the same general area, different sets of plots, with some overlap, were re-sampled across years. Fire-severity varied in sampled plots across years: those sampled in 1988 had not been subject to fire for many decades; only plots burned at high severity were sampled in 1999; plots sampled in 2003, 2008, and 2016 experienced a wide range of fire-severities.

Table 1: Sampling design: plot type, year established, and number of plots sampled in different years. The Rattlesnake and Horseshoe Two Fires occurred in 1994 and 2011, respectively.

Plot Type	Established	Sample Year				
		1988	1999	2003	2008	2016
Pre-fire	1988	26				26
Rattlesnake Fire +5 yrs	1999		12			
Rattlesnake Fire +9, +14 yrs	2003			32	16	19
New	2016					23
TOTAL		26	12	32	16	68
Fire-severity		None	High	Low-High	Low-High	Low-High

We resampled Sixty-eight plots in 2016. Twenty-six of these had been sampled in 1988 [54, 60], before the two fires. Twelve plots were sampled in 1999 to assess vegetation response five years after the RS Fire of 1994; these were not sampled again. Thirty-two plots were sampled in 2003 in the same area, 9 years after the fire, and 16 of those were resampled 14 years after the fire, in 2008. Of the 2003 Rattlesnake plots, 19 were resampled in 2016. Twenty-three “New” plots were added in 2016 to stratify across fire-severity and topography and to capture sufficient numbers for each of the major pine and oak species. These additional plots were chosen using MTBS maps of fire-severity (dNBR), although the actual plot locations were adjusted based on the feasibility of sampling in the dissected terrain. One important point: contrary to our expectations, all the plots sampled from 1999 to 2008—that is, the post-RS Fire plots—were also burned by the HT Fire. As a result, we were capable of assessing the persistence of conversion from Madrean pine-oak forest to oak shrublands after the RS Fire (and 5 years after the HT Fire) at 14 rather than 22 years post-fire.

Plots were sampled in 2016 along a 25m-long transect, placed perpendicular to the slope for ease of sampling. Plot sizes from earlier censuses were as follows: 50m transects and 20 x 20m quadrats in 1988; 50m transects in 1999; 25m transects in 2003 and 2008. As described below, transect width varied according to species, plant density, and the variable measured.

Plot Environmental Data

We gathered field and raster environmental data to investigate the influence of environmental variation on vegetation response to wildfires. In the field, we recorded the spatial location (latitude, longitude) and elevation (a.s.l. in meters) of each plot with Garmin eTrex GPS units (Garmin International, Olathe, KS). Slope (in degrees), aspect, topographic position (drainage, lower slope, middle slope, upper slope, or ridge top), and slope shape (straight, concave straight, concave, convex straight, or convex) were also recorded at each plot to calculate a Topographic Relative Moisture Index [61], which situated sites on a xeric to mesic gradient (0-60 range). We derived raster environmental data from SRTM (Shuttle Radar

Topography Mission) 1 arc-second (30-m resolution) digital elevation models (DEM) (<https://earthexplorer.usgs.gov/>). Using ArcMap v10.3 [62], we used the DEM data to generate (1) incident solar radiation over the entire year (at hourly intervals for the 15th day of each month of the year) using the ArcGIS solar radiation tool and (2) a multiscalar terrain dissection index developed by Holden, Abatzoglou (63).

Raster delta normalized burn ratio (dNBR) data were used for estimating plot fire-severity in the HT Fire [<http://www.mtbs.gov/data/customquery.html>; 64] and examining the influence of fire-severity on vegetation response. We also assessed fire-severity in the field based on tree mortality estimates for all trees >20 cm DBH: no fire: 0% tree mortality; low severity: 1-33%; moderate severity: 34-67%; and high severity: >67%. Out of 67 plots for which MTBS designated a fire-severity classification, 59 were in the same class as the field-based determination and 8 differed. Of those not matching, all were off by only one class, and 6 of those plots were on the geographical border of the two classes. For only two plots were the field-based and MTBS classifications clearly different. These results suggest that raster dNBR for the HT Fire appropriately captured fire-severity at this site [*sensu* 65]. Thus, we used dNBR as an independent variable for all the statistical analyses herein because it was a continuous variable measured soon after the fire, whereas our ground-based assessments were categorical and taken five years post-fire.

Canopy cover was estimated using hemispherical photographs taken with an iPhone 5 at 5, 10, 15, and 20 m along the central 25-m transect line from a height of 1 m for 63 of the 68 plots using CanopyApp (Version 1.0.2, November 7, 2014, ©University of New Hampshire), which has a built-in gyroscope for leveling. Missing values for the 5 plots with no canopy cover data were imputed using multivariate imputation by chained equations in the mice package of R [66]. We took a 100-cm³ sample of mineral soil from 0-10 cm depth (after brushing away the O horizon) at these same four points along the central transect for the same 63 plots, and missing values were similarly imputed. Litter depth to mineral soil was measured (to the nearest 0.5 cm) at 12 equidistant points along the transect lines using a go-no-go device.

Soil was oven-dried to a constant mass in a 70 °C drying oven, and bulk density was calculated as the ratio between soil dry mass and wet volume. Dried soil samples were sifted using a 20-mm mesh sieve, and then homogenized using a mortar and pestle. We then analyzed soil %C, %N, and C: N on a CE Elantech Flash 1112 Elemental Analyzer ($n = 272$).

We examined relationships among environmental variables and fire-severity with mixed-effects models, using the lme function in the lme4 and lmerTest packages in R. This approach accounted for the nested sampling design and the covariance structure of the data. Random effects were designated for the intercept and the slope of the sample replicate nested within sample plot. In all statistical analyses, including these, the residuals of each model were inspected for deviations from homoscedasticity, and all final models contained residuals without obvious deviations from normality. The linearity of all the models held for all interactions except the relationship between canopy cover and dNBR, which was curvilinear in shape, and modeled using a second order polynomial function.

Plot Vegetation Data

For all of the 68, 2016 plots, woody plant species cover was estimated in 4- by 25-m belt transects, averaging values taken at 7.5 and 17.5 m, on the following scale: 0 – absent, <1, 1-9, 10-24, 25-49, 50-75, >75% which matched the 1988 plot inventory protocol [54]. For each of the 68 plots sampled in 2016, live stems of pines were sampled in 25 x 20 m plots, oaks in either 25

x 20 m or 25 x 4 m plots depending on stem density. Each stem was identified to species and as either a survivor of the Horseshoe Two Fire, a resprout from root stock after top-kill, or a seedling emerging after fire. For pines and oaks, diameter at breast height (1.4 m; DBH) was measured (to the nearest 0.1 cm) for stems ≥ 2 m in height that survived the HT Fire. For trunks divided below 1.4 m height, each stem was considered a separate tree. Height (to the nearest cm) was recorded for stems < 2 m. Because resprouting oaks produce many ramets, each genet was counted as a single individual, and the height of the tallest ramet was measured for each genet. The number of ramets for each genet (stems within 50 cm of others) was estimated using the following classes: 0-4, 5-9, 10-49, > 50 stems. We calculated the density and basal area of survivors, the density of seedlings and resprouts recruited after fires, and the heights of recruited stems in each sample plot. Abundance of juvenile pines and oaks was quantified in 1988 in either 20 x 20m quadrats or 50m x 4m belt transects; in 1999 in 50m transects, 5m wide for oaks and 20m wide for pines; in 2003 and 2008 in 25m transects, 2m wide for oaks and 10m wide for pines. Data for juvenile abundance were standardized on a per ha basis to account for variation in plot sizes and for comparisons across species, plots, and years.

To analyze community-level vegetation patterns, we carried out two sets of non-metric multi-dimensional scaling (nMDS) ordinations using PC-Ord software v6 [67]. To assess vegetation changes from pre-fire (1988) to after both fires (2016), we analyzed 26 plots sampled in both years. To examine the influences of fire-severity and other environmental variables on spatial variation in post-fire plant species composition, we analyzed all 68 plots with data from 2016. For both analyses, we evaluated (1) the degree to which the first two axes explained variation in community composition, (2) the loadings of individual species along axes, and (3) the statistical relationships of a suite of field-measured and derived environmental variables with the first two nMDS axes to explore possible environmental drivers of spatiotemporal community variation. For the nMDS of pre-fire (1988) vs. post-fire (2016), we also employed (1) t-tests to assess significant changes over time in plot scores for Axes 1 and 2 and (2) simple linear regressions to examine whether plots experiencing higher fire-severity (dNBR) exhibited greater change in plot scores over time for both nMDS axes.

To examine the impact of the HT Fire on the survivorship of pines and oaks, we used the 2016 data to calculate the basal area and density for survivors of each species, pines combined, oaks combined, and all trees combined. We examined the relationship of these two dependent variables with fire-severity using a general linear model and a gamma distribution, because of the abundance of zeros in overdispersed, non-count data.

We examined differences in pine and oak recruitment across sample periods, from 1988 (before the two fires) to after the RS Fire (1999, 2003, 2008) and after the HT Fire (2016). As described previously, juvenile density was sampled in the same general area, with some plots resampled over multiple periods, and some not (Table 1). We tested four specific hypotheses: (1) did juvenile density change from 1988 to 2016 (i.e. before vs. after the two fires) for *P. leiophylla* and *P. engelmannii*, the only two species for which data were collected for both years?; (2) did recruitment differ between pines and oaks (and among species) for each of the four post-fire sampling periods (1999, 2003, 2008, 2016); (3) did the relative recruitment of pines and oaks differ after the RS vs. the HT Fires?; and (4) did the higher density of oak vs. pine recruitment 5 years after the RS Fire ([1]) endure after 9 and 14 years? We tested hypotheses for individual species using hurdle Poisson mixed effects models using the glmmTMB R package [68]. We tested hypotheses involving pines vs. oaks, data sets which included very few zeroes, with paired t-tests using the t.test function of psych in R [59], separately for each sample year

because different sets of plots were sampled over time.

We tested for differences in the height of resprouts and seedlings among species for 5, 9, and 14 years after the RS Fire (1999, 2003, 2008) and 5 years after the HT Fire (2016) using mixed-effects models. Plots and year were treated as random factors; fixed effects were species, juvenile type (seedling vs. sprout), and the interaction of species and type with year. We tested for an association of species and number of resprouts per genet using Chi-square tests.

Finally, we tested hypotheses about the relationships between juvenile abundance and the field-measured and extracted environmental variables for the 68 plots sampled in 2016 using hurdle regression in the *pscl* package in R to accommodate count data with many zeros. Each hurdle model was evaluated for overdispersion and either negative binomial or Poisson models were chosen based on significance of the theta terms.

Plant Functional Traits

We examined the relationship between the post-fire pine-oak regeneration dynamics and tree ecophysiology by measuring a suite of physiological characteristics on juvenile pines and oaks that had regenerated following the HT Fire. Since all sample sites had returned after the RS fire, we were unable to take measurements on trees that had burned in the first fire, but survived the second fire—which was the proposed sampling design in our original proposal. Thus, all measurements were taken on 5-year-old post-fire recruits. In addition to examining species-specific differences in post-fire plant performance, we evaluated whether fire severity and topographic position influenced tree physiology.

Physiological measurements were taken in late May and early June 2016, just prior to the onset of the North American Monsoon, when plants typically experience the greatest drought stress. Physiological measurements were taken on the four-target species that experienced major shifts in dominance in the vegetation monitoring plots (*P. engelmannii*, *P. leiophylla*, *Q. hypoleucoides*, and *Q. arizonica*). Measurements were taken on four individuals of each of the four target-species in a subsample of 24 of the 63 permanent vegetation plots that we inventoried in 2016 ($N = 384$ individuals). All individuals were post-fire recruits following the HS Fire (pines were seedlings and oaks were resprouts). Measurements were taken across the fire severity gradient, spanning from low- to high-severity, and across the topographic gradient spanning from valley bottom to ridgetop. All specimens were sampled from just outside of the vegetation plots to minimize destructive sampling effects on the long-term monitoring plots. Maximum photosynthesis (A_{\max}), stomatal conductance (g), and transpiration rates (E) were measured *in-situ* on healthy leaves using an open-system portable infrared gas analyzer (Welles 1986) (LI-6400, LiCor, Lincoln, Nebraska, USA) under saturating light ($800 \mu\text{mol m}^{-2} \text{s}^{-1}$, as determined by Barton and Teeri 1993 Barton and Teeri (69)) using the LED attachment for the LI-6400 photosynthesis system. Instantaneous intrinsic water use efficiency of the leaf ($i\text{WUE}_{\text{leaf}}$) was also calculated as maximum photosynthetic rate over stomatal conductance (A_{\max}/g). All gas exchange measurements were taken in the morning prior to midday stomatal closure. For the pines, we spread needles in one flat layer to fill the 2 x 3 cm chamber. Individual oak leaves were large enough to fill the chamber entirely.

Leaf spectral reflectance was measured using a UNISpec Spectral Analysis System (PP Systems, Haverhill, Massachusetts, USA) over the range of 400–1000 nm with a 2.0 mm diameter foreoptic and an internal 6.8 W halogen lamp. Standard controls were dark and a spectralon reflectance white standard. The UNISpec unit was recalibrated after every 10 measurements using the reflectance white standard. Leaves were held in a black polyvinyl

chloride clip at a 60° angle relative to the foreoptic for scanning. For the pines, we arranged needles in a flat layer in the foreoptic leaf clip for each specimen. Oak reflectance was taken on the adaxial (top) side of the leaf. Leaf mass per unit area (LMA) was calculated by scanning fresh leaves using the Turboscan app on an iPhone6 and by calculating leaf area using ImageJ software (<https://imagej.nih.gov/ij/>). For the pines, leaf area was estimated for 1 fascicle of needles; for the oaks, one healthy leaf was scanned for each individual. LMA was taken as leaf dry mass (DM) (after drying to a constant mass in a 70°C oven) divided by leaf area. Leaf relative water content (RWC) was determined on one whole leaf of each individual by measuring its fresh mass (FM), saturated mass (SM) after immersing them in distilled water in the dark for 24 h, and DM (described above). RWC was calculated as: $RWC = (FM - DM) / (TM - DM) \times 100$. Leaf chlorophyll (CHL) and anthocyanin (ANTH) content were measured using hand-held meters (model CCM-300 for CHL, and model ACM-300 for ANTH, Opti-Science, Inc. USA) on light-adapted leaves using the same method for pines, as described previously. All measurements were taken on the same leaves to avoid variation among leaves of the same individual.

Temporal changes in carbon isotope discrimination were estimated for each year following the HS Fire on annual rings of two post-fire recruits of each of the four-target species at low, moderate, and high fire severities following English, McDowell (70) (i.e. 2 individuals of each species in each fire severity-class for each year of growth from 2011-2015, $N = 32$ individuals and 160 tree-ring samples). We were unable to report the proposed $\delta^{18}O$ analysis due to instrumentation problems at the Yale Isotope Lab, which was processing our samples at the internal Yale rate. Due to budgetary and labor constraints for processing more samples, we were unable to analyze the $\delta^{18}O$ samples elsewhere, so the report includes results for only the $\delta^{13}C$ analyses. Total $\Delta^{13}C$ with atmospheric corrections for wood isotope values ($\delta^{13}C_{plant}$) and intrinsic water use efficiency ($iWUE_{wood}$) were calculated for each year of growth for each juvenile using the carbon isotope ratios measured in the tree rings ($\delta^{13}C_{plant}$), annual estimates of atmospheric $\delta^{13}C$ ($\delta^{13}C_{atm}$), and annual atmospheric CO_2 concentrations (C_a). $\delta^{13}C_{atm}$ values were obtained from <http://www.esrl.noaa.gov/gmd/dv/data/> (accessed 12/21/17), and C_a data were taken from http://scrippsco2.ucsd.edu/data/atmospheric_co2/ (accessed 12/21/17) for each year of juvenile tree growth. $\Delta^{13}C$ discrimination was calculated using the equation by Farquhar and Sharkey (71): $\Delta = \frac{\delta^{13}C_{atm} - \delta^{13}C_{plant}}{1 + \delta^{13}C_{plant}/1000}$ for each tree-ring for each plant specimen. We calculated intrinsic water use efficiency of the xylem ($iWUE_{wood}$) following McCarroll and Loader (72): $iWUE_{wood} = \frac{C_a * (\Delta - a)}{1.6 * (b - a)}$ where a is the constant associated with fractionation during CO_2 diffusion through the stomata (4.4‰; [73]), and b is the constant associated with fractionation during carboxylation (27‰; [74]), and C_a is atmospheric concentration of CO_2 for that year of tree-ring growth.

Yearly PDSI values were regressed onto $\delta^{13}C$ values for the years following the fire events to examine the relationship between C isotope discrimination and PDSI to examine how differences in post-fire climatic conditions may have influenced post-fire tree regeneration. $\delta^{13}C$ analyses were performed on a small subset of the plots including 2 individuals of each species from just outside 2 plots per burn severity class (low, middle, high). Four individuals of each species were destructively sampled with a handsaw at the base and complete cross-sections were sanded to a high polish for whole-wood $\Delta^{13}C$ values based on English, McDowell (70) who determined that cellulose digestion was not needed for such analyses. Annual tree ring samples were extracted using a dental drill and $\delta^{13}C$ values were assessed at the Yale Isotope Lab (New Haven, CT). Since all sites that burned in the RS Fire had also burned in the HT Fire, we were

limited to destructively sampling only post-HY Fire recruits, as we found no juveniles that had regenerated after the RS Fire and had also survived the HT Fire.

We used mixed-effects models, using the lme function in the lme4 and lmerTest packages in R to test for differences in pine and oak physiology 1) at the species-level, 2) among fire severities (low, moderate, or high), 3) among topographic positions (lower, middle, or upper), and 4) for the interaction between fire severity and topographic position. Mixed models were also used to examine temporal changes in $\Delta^{13}\text{C}$ isotope discrimination and $\text{iWUE}_{\text{wood}}$ among species and fire severities. This approach accounted for the nested sampling design of four individuals per species per sample site. Random effects were designated for the intercept and the slope of the sample replicate nested within sample plot.

Results

Climate and Fire Patterns in Southeastern Arizona (1895-2015)

June-August Palmer Drought Severity Index (PDSI) varied substantially from 1895 to 2015 in southeastern Arizona (Figure 2). The region was exceptionally arid from 1994, the year of the Rattlesnake Fire, to 2015, significantly lower than that for the rest of the time-series from 1895-1993 ($t=-2.07$, $P=0.04$). Thirteen of those years were below -2 PDSI, 7 were 0 to -2, and only two were above zero.

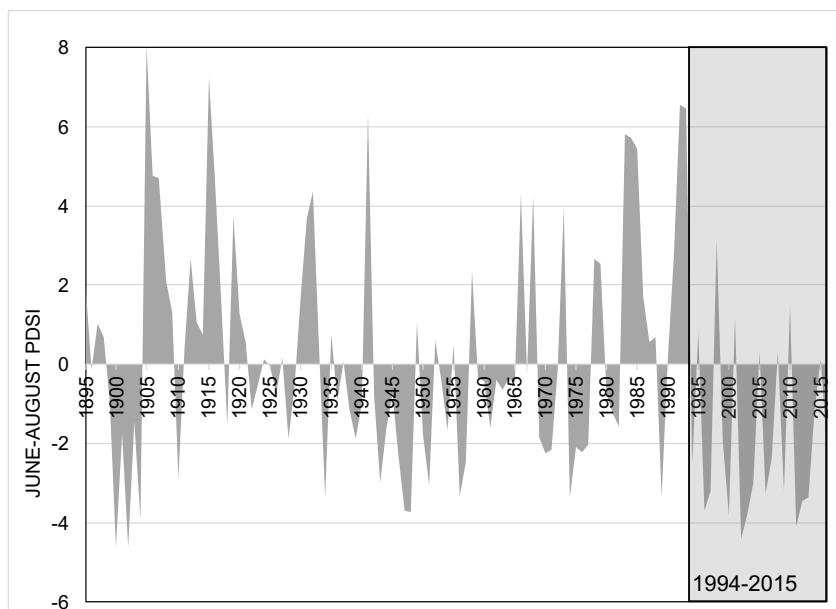


Figure 2: Growing season (June-August) Palmer Drought Severity Index (PDSI) for 1895-2015 in southeastern Arizona. Shaded area highlights the period 1994 to 2015, which was significantly drier compared to the period before 1994 ($t=-2.07$, $P=0.04$).

The number of fires and area burned also varied greatly from 1921 to 2015 in the region (Figure 3). Area burned per year was significantly higher from 1994 to 2015 compared to the period prior to the Rattlesnake Fire (1921-1993; $t=2.10$, $P=0.038$). The number of fires per year did not differ between these two periods ($t=0.84$, $P=0.40$).

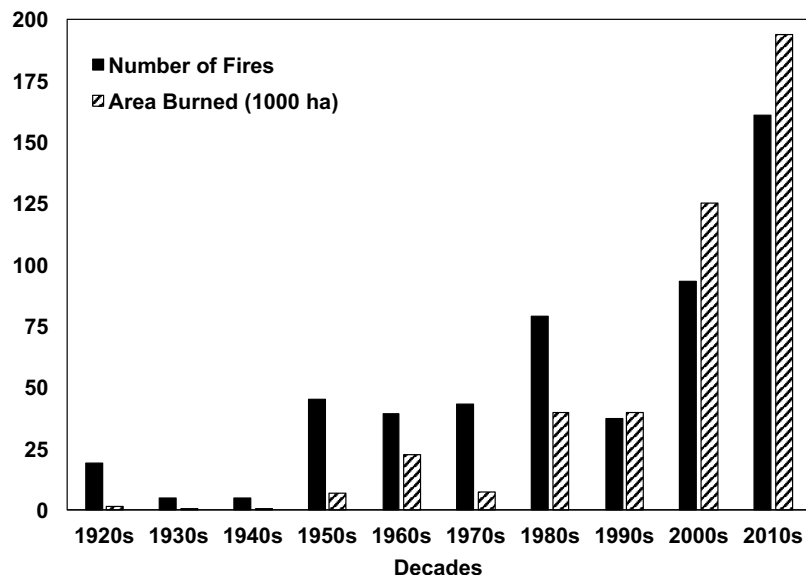


Figure 3: Number of fires and area burned by decade for Coronado National Forest, southeastern Arizona. Data from fire atlas [57].

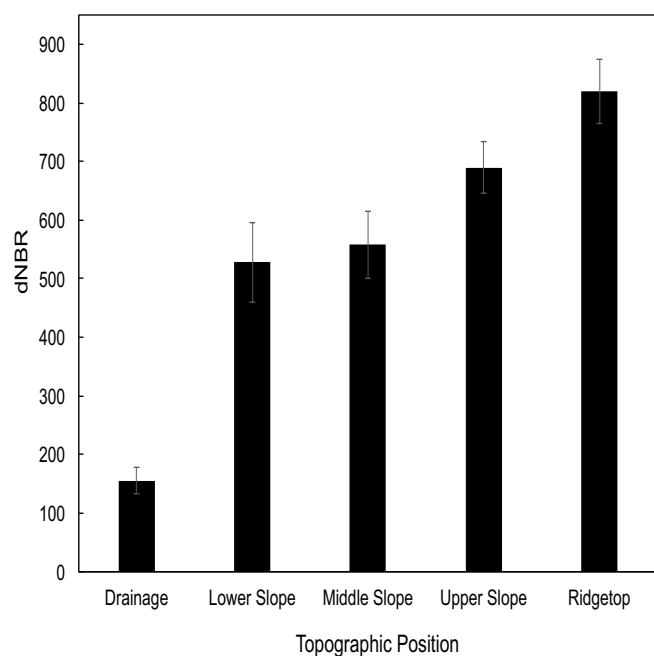


Figure 4: Mean (± 1 SE) for fire-severity (dNBR) for five topographic positions, from less to more exposed. Mean dNBR differed significantly across groups ($df=4, 62, t=14.96, P<0.0001$).

Environmental Variables in Relation to Fire-Severity (2016)

Fire-severity (dNBR) in the HT Fire increased from less to more exposed sites (Figure 4). Drainages and ridgetops stood out as especially low and high in fire-severity, respectively. Canopy cover exhibited a significant curvilinear relationship with fire-severity, with the most open plots occurring at moderate fire-severity. Plots were shaded by mature trees after low-severity fire, oak resprouts and other shrubs after high-severity fire, and a mix of the two after moderate-severity fire. Litter depth and percentage soil C and N were significantly negatively related to fire-severity and elevation and positively related to TRMI (moisture) ($P<0.05$). C: N and bulk density did not vary significantly with any of the three independent variables ($P>0.05$)

Plant Community Patterns over Time and Space (1988-2016)

For the nMDS for the 26 plots sampled in 1988 and 2016 (Figure 5A), Axis 1 accounted for 17% and Axis 2 63% of the variance in community composition. Woody plant community composition changed drastically from before (1988) to after (2016) the RS and HT fires. Plots from 1988 fell primarily on the left (low scores) and 2016 plots primarily on the right side (high

scores) of Axis 1 (Figure 5A). Plot scores declined significantly between the two sample periods for both Axis 1 ($df=25$, $t=6.51$, $P<0.0001$) and Axis 2 ($df=25$, $t=11.05$, $P<0.001$). Plots experiencing higher fire-severity exhibited more drastic change over time in community composition (Axis 1: $df=24$, $t=1.76$, $P=0.046$, $r=0.34$; Axis 2: $df=24$, $t=2$, $P=0.02$, $r=0.38$). The 1988 to 2016 change along Axis 1 largely represents a shift away from conifers towards oaks, graminoids, and *Yucca madrensis*. Axis 2 also reflects a decrease in conifers. Environmentally, Axis 1 transitions from open, low-elevation plots with low fire-severity to the opposite, whereas Axis 2 represents a gradient from shady plots with high fire-severity to more open plots with low fire-severity.

For the nMDS of all 68 plots sampled in 2016 (Figure 5B), Axis 1 accounted for 29% and Axis 2 58% of the variation in community composition. Axis 1 revealed a strong shift from a diverse suite of species, including pines, *Juniperus deppeana*, and lower elevation oaks (*Quercus emoryi* and *Q. arizonica*) to a species-poor, shrubby community mainly of upper elevation oaks, *Q. hypoleucoides* and *Q. rugosa*, and the shrub *Ceanothus fendleri*. This transition was correlated most strongly with increasing fire-severity, but also with increased topographic exposure, including elevation, slope, TRMI, and land dissection (Figure 5B). Axis 2 revealed a shift from conifers, *Arbutus arizonica*, and low-elevation shrubs (*Mimosa biuncifera* and *Baccharis sergiloides*) to graminoids and the higher-elevation shrubs *Ceanothus fendleri* and *Brickellia californica*. This transition was correlated with increasing elevation and fire-severity and decreasing litter depth (i.e. more exposed sites).

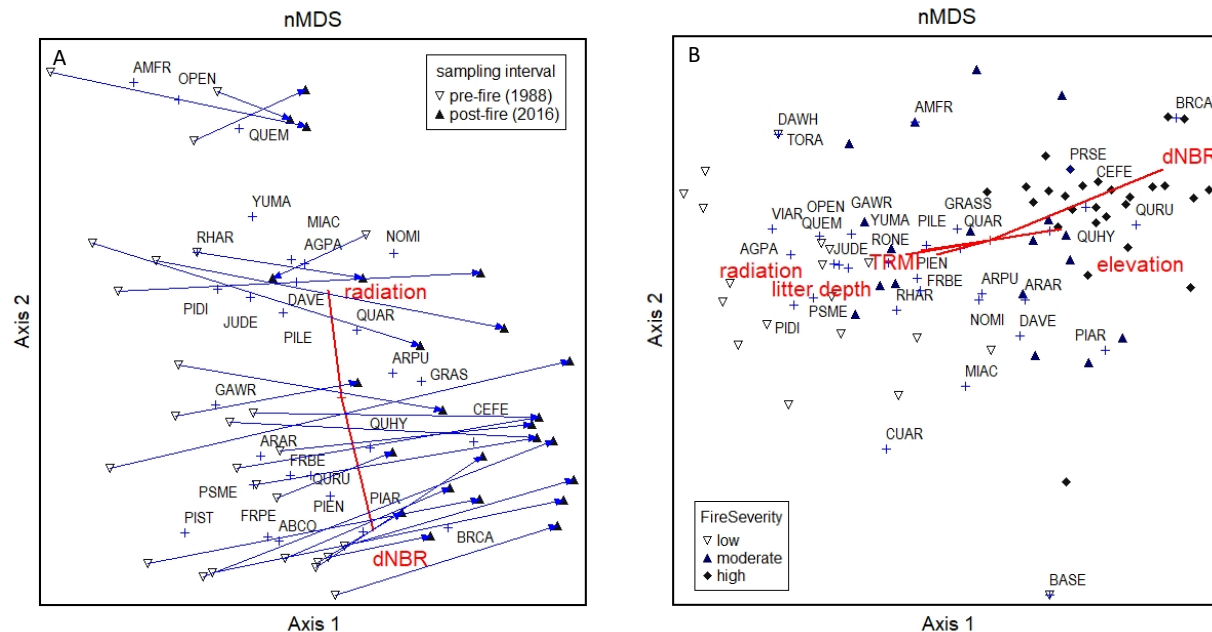


Figure 5: Positions of plots and species with respect to two axes from non-metric multidimensional scaling analysis. (A) 26 plots sampled before (1988) and after (2016) the two large fires, dates connected by a time line for each plot and (B) 68 plots sampled in 2016. Vectors show the environmental variables most strongly correlated with axes.

Pine and Oak Recruitment Before and After Fires (1988-2016)

Patterns of recruitment differed from before to after fires, between pines and oaks, and between resprouts and seedlings (Table 2). Prior to the fires (1988), when only pines were

sampled and seedlings and resprouts were not distinguished, juvenile pines were abundant. Pine recruit density then declined by more than an order of magnitude for the samples taken from 1999 to 2016 after first the Rattlesnake and then the Horseshoe Two Fire (Table 2). Juvenile density was significantly lower in 2016 compared to 1988 for plots sampled during both years for *P. leiophylla* (hurdle regression/negative binomial: $z=-6.05$, $P<0.0001$) and *P. engelmannii* (hurdle regression/negative binomial: $z=-3.21$, $P=0.001$).

Table 2: Mean (± 1 SE) density (per ha) of recruits for pines and oaks for five sample periods. “sdlgs”: seedlings; “sprts”: sprouts; “all”: seedlings + resprouts. The Rattlesnake and Horseshoe Two Fires occurred in 1994 and 2011, respectively. Statistical differences between densities of seedlings vs. resprouts are shown for each species-year combination on the resprout mean (hurdle regression; ^{ns} $P>0.05$, $*P<0.05$, $**P<0.01$, $***P<0.001$). Other statistical results are given in the text. Different sets of plots were sampled across time; see Table 1 for details.

Recruit Type	1988	1999	2003	2008	2016
	453.95	16.67	7.5	12.5	31.76
<i>P. engelmannii</i> sdlgs	-90.81	-5.95	-3.33	-7.93	-9.36
<i>P. leiophylla</i> all	764.71 -184.11				
		60	63.75	112.5	67.94
<i>P. leiophylla</i> sdlgs		-30.55	-17.68	-23.16	-14.52
		93.33 ^{ns}	42.50 ^{ns}	52.50*	41.47 ^{ns}
<i>P. leiophylla</i> sprts		-19.9	-8.97	-9.46	-5.61
		86.67	12.5	15	99.12
<i>Q. arizonica</i> sdlgs		-34.05	-5.22	-8.06	-21.35
		36.67 ^{ns}	55.00***	45.00***	323.82***
<i>Q. arizonica</i> sprts		-24.35	-15.42	-23.06	-39.95
		63.33	72.5	130	230.59
<i>Q. hypoleucoides</i> sdlgs		-24.84	-14.52	-19.62	-86.42
		1030.00** *	820.00***	805.00***	1617.94** *
<i>Q. hypoleucoides</i> sprts		-70.69	-40.64	-51.36	-135.51
		156.67	113.75	177.5	141.18
All <i>Pinus</i>		-43.33	-22.66	-28.74	-20.55
		1216.67	960	995	2321.47
All <i>Quercus</i>		-56.88	-43.64	-43.06	-206.81
# of Plots	PILE=17 PIEN=19	12	32	16	68

For every survey from 1999 to 2016 (Table 2), combined recruitment of oaks was much higher than that for pines sampled in the same plots: five years (2016) after the HT Fire ($df=67$, $t=10.32$, $P<0.0001$) and five years (1999: $df=11$, $t=13.04$, $P<0.0001$), nine years (2003: $df=31$, $t=14.10$, $P<0.0001$), and 14 years after the RS Fire ($df=15$, $t=11.98$, $P<0.0001$). Density of recruits did not differ between the two fires, except for *Q. hypoleucoides*, which exhibited higher density for the HT Fire ($z=2.17$, $P=0.03$).

Juvenile density was substantially higher for resprouts than seedlings in *Q. arizonica* and *Q. hypoleucoides*, except for 1999 (Table 2). *P. leiophylla* seedling density was higher than for resprouts in 2008, but not significantly different for the three other sample periods (Table 3). *P. engelmannii* did not resprout after fire.

The number of ramets per resprouting genet differed among species. Ninety-seven percent of resprouting *P. leiophylla* produced only 0-4 ramets per genet (mostly a single one), far less than for any of the oaks ($P<0.05$). *Q. hypoleucoides* produced more ramets per resprouting genet than any other species ($P<0.05$), with over 56% producing more than four stems.

Post-fire heights of juvenile plants differed significantly among species ($df=3,3713.3$, $F=40.13$, $P<0.0001$; Figure 6), differences that increased from 1999 to 2008 after the Rattlesnake Fire (interaction: $df=3,3713.3$, $F=39.36$, $P<0.0001$). In almost all circumstances, oak juveniles were taller than those of pines—for comparisons of resprouts to resprouts, seedlings to seedlings, and resprouts to seedlings. *Q. hypoleucoides* produced significantly taller resprouts than any other species. *P. leiophylla* resprouts were taller than seedlings of *P. engelmannii*. Seedling height did not differ among pines or oaks (Figure 6). Resprouts were much taller than seedlings ($df=3,3720.3$, $F=447.96$, $P<0.0001$), and the degree of this difference depended on year ($df=3,3720.4$, $F=442.13$, $P<0.0001$), notably increasing from five to 14 years during the recovery after the RS Fire.

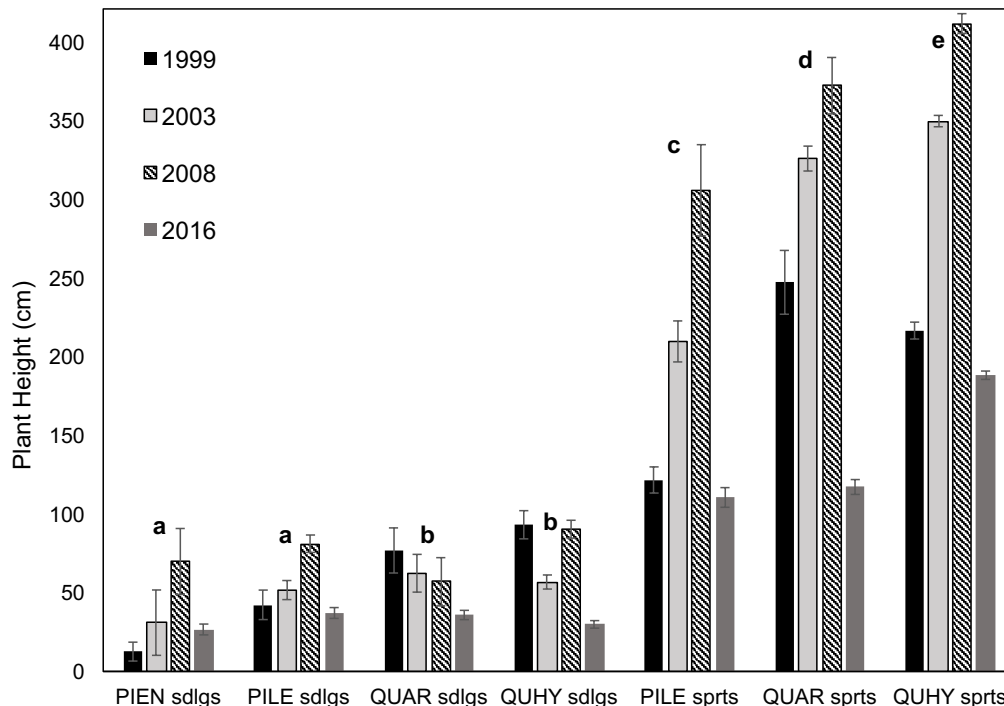


Figure 6: Heights of seedlings and resprouts for pines and oaks after the Rattlesnake Fire (1994) sampled in 1999, 2003, and 2008 and the Horseshoe Two Fire (2011) sampled in 2016. PIEN: *P. engelmannii*, PILE: *P. leiophylla*, QUAR: *Q. arizonica*, QUHY: *Q. hypoleuroides*; sdls: seedlings; sprts: resprouts. Sample plots overlapped, but were not identical across years. Species with different letters exhibited statistically significant differences in height.

Pine and Oak Recruitment in Relation to Fire and Environmental Factors (2016)

Pine and oak recruitment in 2016 was significantly affected by environmental factors, including fire, but these effects differed by species and for seedlings vs. resprouts (Appendix D). In general, seedling recruitment declined with increasing fire-severity and increased with soil moisture (TRMI). *P. leiophylla* resprout abundance also declined with fire-severity, but this pattern was marginally insignificant. In contrast to seedlings, recruitment of oak resprouts increased with fire-severity (and elevation) and decreased from drier to moisture sites.

Plant Physiological Responses

Post-fire pine and oak physiology was species-specific, and surprisingly, it was not significantly influenced by topographic position or fire severity (ns, data not shown). The maximum photosynthetic rate (A_{\max}) results were not especially telling; they showed that only *P. leiophylla* had significantly higher A_{\max} values than the other three species ($P < 0.05$). On the other hand, *P. engelmannii* displayed significantly lower transpiration (E) and stomatal conductance (g) and significantly higher $iWUE_{\text{leaf}}$ than the other three other species ($P < 0.05$), which suggests that this species adopts a more isohydric strategy of reduced E and g relative to the more anisohydric *P. leiophylla* and the oaks (Figures 7 and 9). These results mirror the species-level differences in leaf RWC, which differed significantly among all four-study species ($P < 0.05$). RWC was highest for *P. engelmannii*, followed in order by *P. leiophylla*, *Q. arizonica*, and *Q. hypoleuroides*. The leaf spectral reflectance, and CHL and ANTH content analyses were more telling measures of plant photosynthetic potential than A_{\max} , which was likely influenced heavily by the hot, dry conditions of the field sampling timespan which occurred at the peak of the fore-summer drought in the American Southwest. The pines displayed higher leaf spectral reflectance than the oaks throughout the entire electromagnetic spectrum (Figure 8). CHL and ANTH content were significantly higher for *Q. hypoleuroides* than the other three species ($P < 0.05$). ANTH content was significantly higher in the oaks than the pine species ($P < 0.05$). LMA did not differ significantly between pines and oaks ($P > 0.05$).

Temporal changes in $\Delta^{13}\text{C}$ and $iWUE_{\text{wood}}$ isotope discrimination were also species-specific and not well-related to environment (Figure 9). Nor were they significantly correlated with yearly PDSI for the Southwest ($P > 0.05$ data not shown). $\Delta^{13}\text{C}$ values differed significantly among species over the time series ($P < 0.05$), and were much lower for the pines than the oaks in 2011, in their first year of growth immediately after the HT Fire. $\Delta^{13}\text{C}$ values increased in subsequent years in *P. engelmannii* to approximate the consistently high $\Delta^{13}\text{C}$ values for *Q. hypoleuroides* in all years since the fire event. In contrast, $\Delta^{13}\text{C}$ remained low for *P. leiophylla* for all post-fire years. As in most of the other physiological measures, *Q. arizonica* displayed intermediate $\Delta^{13}\text{C}$ values. Temporal $iWUE_{\text{wood}}$ patterns mirrored those of $\Delta^{13}\text{C}$.

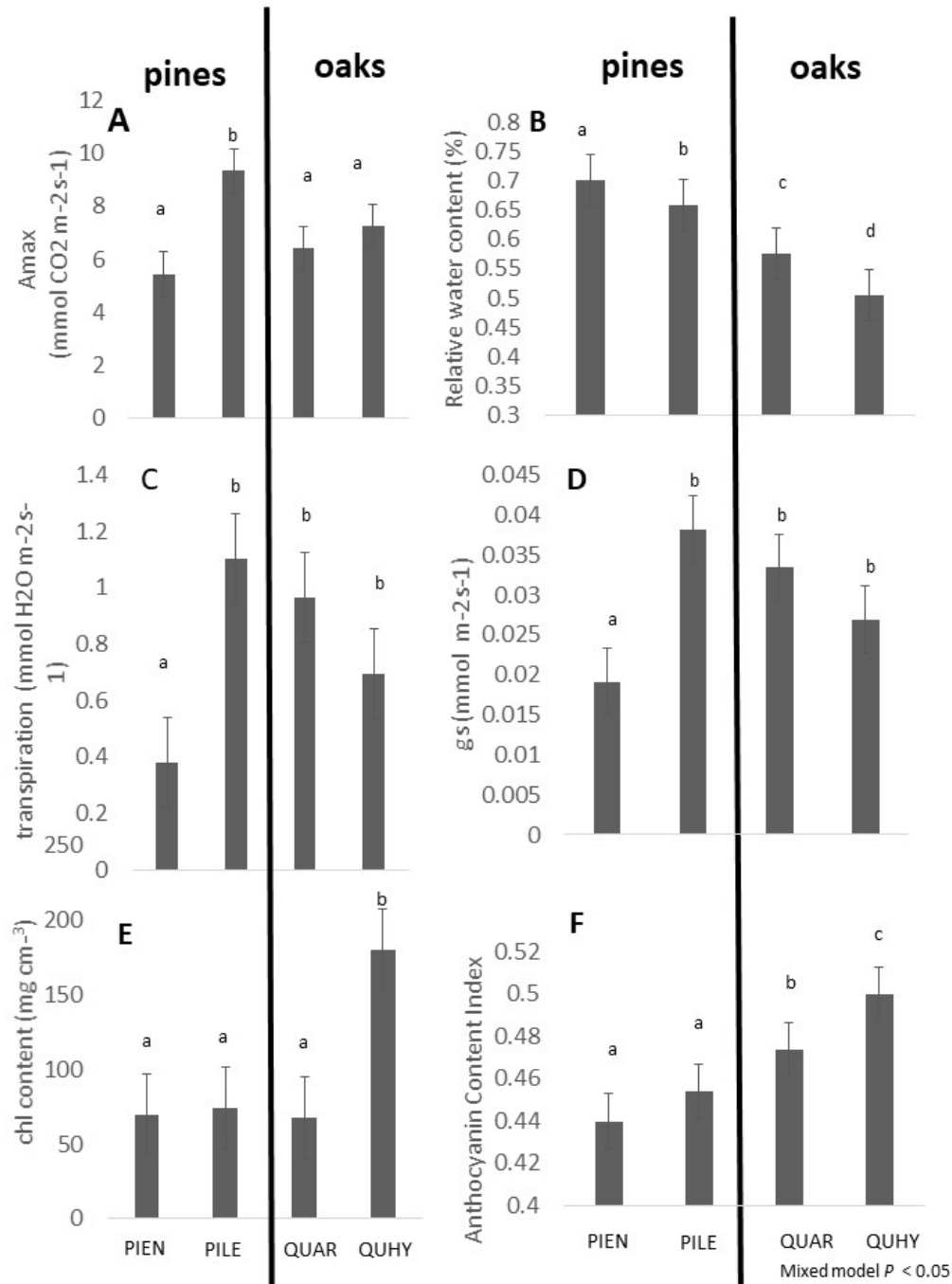


Figure 7: Mean \pm S.E. values of A) maximum photosynthetic rate (A_{max}), B) leaf relative water content (RWC), C) transpiration rate, D) stomatal conductance, E) chlorophyll content (chl), and F) anthocyanin content by species. Species are abbreviated as follows: PIEN = *Pinus engelmannii*, PILE = *P. leiophylla*, QUAR = *Quercus arizonica*, and QUHY = *Q. hypoleucoides*. All parameters differ significantly among species according to mixed-models analyses, and significant pairwise differences among species are indicated with letters. Species that do not share the same letter differ significantly at the $P < 0.5$ -level.

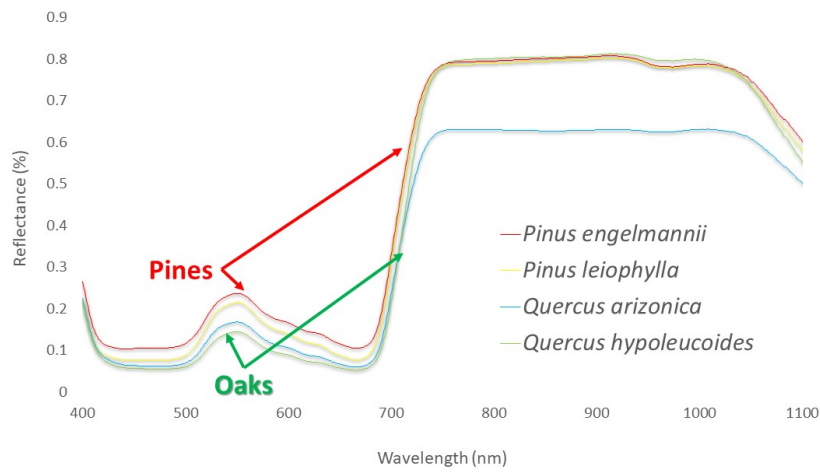


Figure 8: Leaf spectral reflectance (%) for the four-study species across the wavelengths ranging from 400-1100 nm.

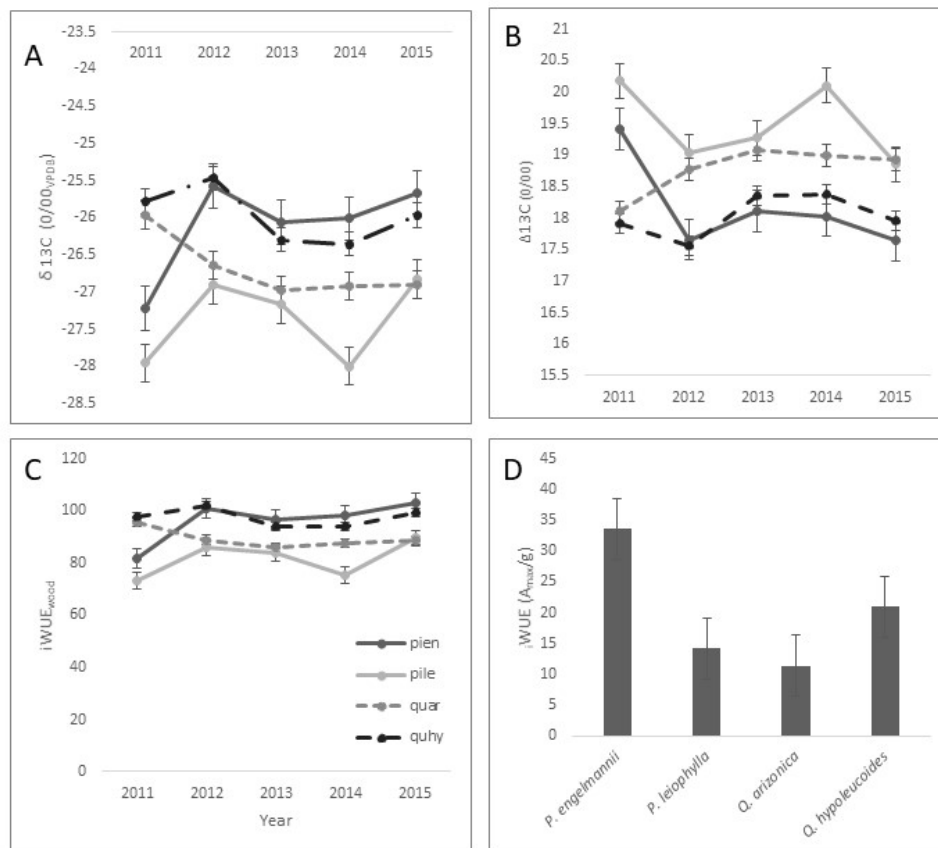


Figure 9: Carbon isotope results for A) $\delta^{13}C$ of xylem tissue, B) $\Delta^{13}C$, and C) intrinsic water use efficiency ($iWUE_{wood}$) and D) instantaneous water use efficiency of the leaf ($iWUE_{leaf}$) for each year of juvenile growth of *P. engelmannii* (*p. eng*), *P. leiophylla* (*p. lei*), *Quercus arizonica* (*quar*), and *Q. hypoleucoides* (*quhy*), respectively.

Discussion

Our results highlight the impacts of contemporary high-severity wildfire on forest stand structure and plant community composition in Madrean pine-oak forests in the American Southwest. The current post-fire vegetation is the product of a shifting fire regime over the last several centuries that can be divided into three distinct eras: (1) historically frequent surface fires before Euro-American settlement [10, 11, 38] that favored an open forest with a mix of pines and oaks [36, 40, 46, 75]; (2) a 20th century period with few fires as a consequence of livestock grazing and active fire suppression that led to landscape-scale fuel accumulation; and (3) a contemporary era of large, high-severity wildfires. Below, we address the four main questions in our proposal that examine the consequences of this most recent period, discuss the potential additional role of drought in our findings, and suggest future scenarios and management implications.

Question 1: Does conversion of Madrean pine-oak to oak shrubland after high-severity fire persist over the long term and after a second large, high-severity fire?

Fire regime shifts, as described previously, are directly responsible for the conversion of Madrean pine-oak forest to an oak shrubland-dominated landscape. As predicted, predominance of post-fire vegetation by oak resprout shrubland persisted for at least 14 years after the RS and 5 years after the HT fires. Regeneration results after five years were a good predictor of patterns after 14 years [see 76]. As expected, the degree of post-fire dominance by oaks was consistent between the two fires. The substantial advantage of oaks in terms of number, height, and vigor of recruits strongly suggests continued oak dominance.

Vegetation conversion was evident at both the community- and population-levels. The nMDS analysis revealed a transition from typical Madrean pine-oak forest before (1988) to an oak shrubland after (2016) the two crown fires. Similar compositional change occurred spatially from low- to high-severity fire sites after the HT Fire. The ordination analysis revealed the importance of elevation and topographic position in organizing communities. However, fire-severity was more strongly correlated with ordination plot scores for both of the first two axes than were elevation or any other topographic variable, suggesting that, at least five years after the HT Fire, wildfire plays the dominant role in structuring vegetation in the Chiricahuas, muting the typical pre-eminent signal of physiography.

At the population level, resprouts of *Q. hypoleucoides*, in particular, dominated nearly all high-severity fire sites, except at lower elevations, where resprouts of *Q. arizonica* and *Q. emoryi* were more abundant. The paucity of pine recruits was striking—across all plots, regardless of fire-severity, and across all sample years from 1999 to 2016, to such a degree that the density of *P. engelmannii* and *P. leiophylla* recruits in 2016 had declined to 7 and 14% of their 1988 pre-fire levels, respectively. Two key attributes of oaks amplified this advantage over pines. First, because oaks produced far more resprout ramets per top-killed stem than did *P. leiophylla*, the actual differential in recruits is much higher than indicated by the genet data. *Q. hypoleucoides* was an especially prolific resprouter, producing more ramets per genet than any other species. Second, recruit height was skewed strongly in favor of oaks after both fires, especially for *Q. hypoleucoides*, and oaks maintained this height advantage and canopy dominance over the 14-year recovery period after the RS Fire. Whereas most oak recruits were tall resprouts, many of the pine recruits were small, recent seedlings. This is likely to lead to higher long-term success of oak compared to pine recruits, even holding density constant.

Spatial patterns of recruitment were directly related to fire-severity in the 2016 analyses.

Post-fire seedling density declined with increasing fire-severity for each pine and oak species, but the opposite trend occurred for oak resprouts. These results provide insight into the mechanisms governing the success of seedlings vs. resprouts and, as a result, pines vs. oaks especially where fire burned at high severity. Relatively low soil N and C, shallow litter, and high levels of competition from thickets of thriving oak resprouts and other shrubs likely created adverse conditions for establishing seedlings, which must build new roots and shoot systems *de novo*, compared to resprouts, which are provisioned from underground resources, allowing them to quickly rebuild photosynthetic biomass [77, 78].

The forest type conversion documented in this project is concordant with a mounting body of work demonstrating that a shift from surface to crown fire regimes often leads to replacement of pines, across a vast region including the Rocky Mountains [2, 23, 25-27, 79, 80], the Sierra Nevada [76, 81], the Sky Islands [1, 82, 83], and the Sierra Madre [36, 84].

Question 2: Does resprouting in *P. leiophylla* rescue populations of this species in high-severity fire environments?

Although resprouting in *P. leiophylla* was largely confined to smaller top-killed stems [Barton and Poulos, unpublished data; 42], it nevertheless provided this species with approximately twice as many post-fire recruits than with seedlings alone, after both fires. Moreover, these resprouts held a considerable height advantage over conspecific seedlings. Even though they were shorter than those of oaks, *P. leiophylla* resprouts remained competitive with co-occurring *Q. arizonica* and *Q. hypoleucoides* during the post-fire recovery period. These results support our original hypothesis that the modest resprouting capacity of *P. leiophylla* may represent a “rescue effect” for this species in areas subject to high-severity fire, where seedling establishment is particularly restricted [see 42].

Question 3: How does pine and oak regeneration vary across the fire severity gradient, and to what extent are these responses mediated by site characteristics, such as physiography?

As predicted, the dominant influence of fire-severity on post-fire tree survival and regeneration was mediated by topography. Fire-severity decreased from ridgetops to slopes to drainages, and, as a result, less exposed, lower elevation sites appear to have served as refugia for pines and perhaps other species sensitive to high-severity fire. Such predictable fire refugia in large fire mosaics, often associated with topography [4, 5, 85, 86], are critical to the maintenance of biological diversity and as foci from which sensitive species may spread back to their previous distributions should fires abate [e.g. 87].

The processes of mortality and recruitment imposed by the HT Fire, then, have led to a restructuring of vegetative communities across the post-fire landscape: oak shrublands are more common on exposed sites and pine-oak forest are now more restricted to protected lower slopes and drainages. Historical shifts in the distributions of pines in relation to fire are difficult to quantify, and the pre-fire distribution of mature pines outside such refugia may have occurred in response to opportunistic establishment of pines during wet, fire-free periods. Thus, a key question is whether pines will reestablish outside of these refugia if a more moderate fire regime and favorable climatic conditions were to occur.

Question 4: To what extent do plant functional traits and tree ecophysiology influence the post-fire response of vegetation to high-severity fire?

Species-specific functional traits provide key insights into the mechanisms responsible for the conversion of Madrean pine-oak forest to oak shrublands after high-severity fire. First

and foremost, the vigorous post-fire resprouting response of the oaks after any fire, regardless of severity, versus the weak post-fire resprouting of *P. leiophylla*, and absence of sprouting in *P. engelmannii* represents a fundamental difference in fire regeneration strategies between the two taxonomic groups. Rapid post-fire recolonization by oak resprouts confer an immediate and sustained competitive advantage over the pines which is a pattern that we observed after both fire events, especially at higher fire severities.

While post-fire regeneration strategies are clearly key determinants of tree species regeneration patterns in Madrean pine-oak forests, the oaks, and *Q. hypoleucoides* in particular, display a contrasting set of leaf physiological traits than the pines that promote their sustained growth and survival in the hot, dry post-wildfire landscape. The drought tolerant (isohydric) strategy of the pines, and of *P. engelmannii* in particular, of maintaining a positive water status through stomatal closure is in stark contrast to the oaks, which appear to have adopted a more drought tolerant (anisohydric) strategy of keeping stomates open during the peak of the fore-summer drought [sensu 88, 89]. Widespread mortality of adult isohydric piñon pines, but survival of anisohydric junipers under drought conditions elsewhere in the American Southwest has been well-documented [90-93]. However, studies documenting such differences in post-fire tree recruits are rare [but see 94, 95]. Mechanisms of mortality relate to the demise of isohydric taxa due to carbon starvation following stomatal closure versus the mortality of anisohydric taxa due to hydraulic failure under moisture stress [91]. While different tree species fall along a continuum between isohydric and anisohydric hydraulic strategies, the anisohydric strategy of continued C-fixation under drought stress generally confers a competitive advantage to those taxa under hot, dry conditions. Thus, the pattern in our results of lower g , E , and $\delta^{13}C_{vpd}$, and higher $\Delta^{13}C$ isotope values in 2011 and $iWUE_{leaf}$ and RWC of the pines relative to the oaks may partially underlie the trend of oak dominance after wildfire in the Chiricahua Mountains.

The yearly $\Delta^{13}C$ values are complex, but early stomatal closure may force Rubisco to reduce discrimination against ^{13}C , leading to the reduction of intracellular C concentrations [74], which is a physiological drought avoidance response that explains similar patterns in pine and pine-oak dynamics elsewhere [96, 97]. The significantly higher $iWUE_{leaf}$ of *P. engelmannii*, highlights the tight stomatal control of this species, but the $iWUE_{wood}$ also indicate that this pattern is variable over time, and that the juvenile pines that successfully recruited and survived through 2016 had lower $iWUE_{wood}$ in 2011 (a year with strong moisture deficits), a trait that has been shown elsewhere to be a crucial drought-tolerance factor. The increase in $\Delta^{13}C$ to a rate that approximated that of *Q. hypoleucoides* in all years following the first year of seedling growth also suggests that once *P. engelmannii* gets established, and survives its first year of growth, that it can continue to grow well in the post-fire landscape.

The higher leaf spectral reflectance and CHL and ANTH content of oaks relative to the pines also point to possible mechanisms of pine-oak forest conversion to oak shrubland. This is especially true for these more-static measures relative to our instantaneous gas exchange measurements because of the hot, dry conditions under-which we took the gas exchange measurements. The higher leaf spectral reflectance of the pines relative to oaks across the entire electromagnetic spectrum demonstrates the higher potential of oak C-sequestration relative to the pines. This, coupled with the higher pigment CHL and ANTH pigment concentrations, are likely responsible for the larger biomass (i.e. multiple ramets per genet) and the higher height-growth of post-fire oak recruits relative to pines. Spectral reflectance is significantly correlated with plant pigment concentrations both for chlorophyll, and the suite of accessory pigments including anthocyanins, xanthophylls, and carotenoids [98, 99]. The higher spectral reflectance of the pines

is typical for less stress-tolerant plant taxa, because both plant pigment concentrations and photosynthetic efficiency decline (as does absorption) under drought stress both for other oak species in southwestern North America [100], and for other tree species as well [101, 102].

Plant species may produce a broad range of phenotypes in response to variation in the abiotic environment [103-105]. We have previously-documented species-level differences in pine and oak physiology in relation to elevational distribution and corresponding environmental conditions [60, 69, 106, 107], yet few studies in this region have examined plasticity in pine or oak plant functional traits within individual species across their distributional ranges [but see 108]. Therefore, the lack of significant differences in tree physiological responses across both fire severity and physiographic gradients was surprising, especially since areas of higher fire severity and upper topographic positions were likely much hotter and drier than low fire severity sites that maintained an intact forest canopy or lower topographic positions that were wetter and received lower incident solar radiation. Alternatively, these results suggest that the four-dominant species display plant functional traits that are fixed, and that they exhibit little phenotypic plasticity in relation to environmental setting. This lack of plasticity may warrant concern, due to the lack of pine regeneration in the post-fire landscape, and the potential inability of pines to compete in a warming climate. Phenotypic plasticity in plant functional traits is likely to play a crucial role under future environmental change [109], and in determining which plants will persist under both a hotter climate and in response to crown fire.

Few studies have applied an ecophysiological approach for understanding plant regeneration patterns following wildfire [but see 94, 95, 110, 111, 112]. Therefore, this study represents an important contribution to fire science and adaptive management both for understanding the mechanisms of post-wildfire type conversion and for guiding post-wildfire forest restoration activities under a continually warming climate.

The Role of Aridity in Forest Type Conversion

Recent increases in fire intensity and area burned in the Southwest have been attributed in part to extreme aridity and climate change [12, 19, 113]. Moreover, a combination of increased aridity and warmth is the prime suspect in increased tree mortality in western North America and globally [9, 114, 115]. Both drought and fire activity intensified dramatically in the Chiricahua Mountains during the 1994 to 2015 period. The results of the current study highlight the indisputable role of fire in type conversion from Madrean pine-oak forest to oak shrubland during this period, but circumstantial evidence suggests an exacerbating role of drought. Several proxy variables for soil moisture, elevation and topographic relative moisture index (TRMI) in particular, were strongly correlated with nMDS axes. Recruitment density for seedlings declined with increasing fire severity, but also independently decreased from moister to drier sites along elevation and TRMI gradients. Moreover, pine establishment was very low not only in sites subject to high-severity fire, but in nearly all plots for all sample periods from 1999 to 2016. Finally, as previously described, differences between pines and oaks in leaf physiological responses to moisture deficit in the field strongly implicate drought in the differential recruitment pattern (Poulos and Barton, in preparation).

The synchronous effects of fire and drought have led to abrupt plant community transitions in ecosystems around the world [116], including in the American Southwest [e.g. 2]. The results of our study suggest that high-severity fire, promoted in part by extreme drought, eliminated nearly all stems, creating conditions in which post-fire vegetation was a product of regeneration rather than a mixture of survival and establishment. Drought, aggravated by the

impacts of crown fire, then curtailed pine regeneration in the post-fire environment, allowing vigorously-resprouting oaks to seize the growing space.

Future Scenarios and Management Implications

Uncharacteristic crown fire and extreme drought are projected to continue into the foreseeable future in the American Southwest [8, 91, 117]. Therefore, we expect to see more Madrean pine-oak forest type conversions and slow recovery of already-affected stands. Coop, Parks (26) and Minor, Falk (83) argue that, given their capacity to readily regenerate after high-severity fire, oak shrublands in the Southwest may well be more resistant and resilient to the contemporary and future fire and climate regimes than are pines. These novel conditions appear to favor the fundamental adaptations of oaks—anisohdry, higher photosynthetic potential, and resprouting—over those of pines—isohdry, lower photosynthetic potential, obligate seeding, thick bark, and weak or no resprouting. Falk (29) punctuated this line of thinking, proposing that uncharacteristic crown fire and drought may be pushing all Madrean pine-oak forests in the Sky Islands to a tipping point, where they abruptly transition to more resilient, permanent oak shrub communities. Put in ecological-niche terms, this argument suggests that the breadth of contemporary conditions that overlap with the bio-climatic envelope of pines in the Southwest is shrinking, leading to a contraction of their distribution and abundance that might be permanent.

On the other hand, pines are notorious for the episodic nature of their regeneration, dependent on synchrony of favorable conditions for pollen production, seed crops, germination, growth, and survival [118]. Such windows of establishment may require exposure of mineral soil by previous fire, an extended period of sufficient moisture, and the absence of fire until juvenile plants reach sizes resistant to fire. As a result, periods between large cohorts are often measured in multiple decades [e.g. 119]. Consistent with this scenario, age structures of *P. leiophylla*, *P. engelmannii*, and *P. arizonica* in the Chiricahuas show high variability in establishment over the past three centuries [40, 46]. This raises the possibility that, given sufficient time, pines will recolonize converted pine-oak stands from the remaining refugial seed sources. Success of these seedlings, however, may depend on the degree to which grasses, oaks, and other shrubs have already fully occupied these sites. In other words, oak shrubland is a possible alternative stable state that once established may be relatively resistant to return to the previous mixed pine and oak vegetation no matter what fire and climate conditions prevail [29, 83, 120].

Given the results of our study and future climate projections, we recommend efforts aimed at protection and restoration of Madrean pine-oak forests. Fuel management, through targeted thinning and prescribed fire could potentially reduce the spread and severity of wildfires, a successful management intervention well-established elsewhere in the Southwest. Protection of pine fire refugia in canyons on US Forest Service and Park Service lands (e.g., Rhyolite, Rucker, West Turkey Creek, South Fork of Cave Creek, Cave Creek above Herb Martyr) would be worthy of special effort in this regard. The goal would be to ensure that future wildfires burn within the historic range of variation in these areas. Spatially-explicit fuel maps and a better understanding of the roles of fuels, fire weather, and topography in controlling fire severity in the complex vegetation of the Sky Island would facilitate these management actions. New research examining historic patterns of fire and regeneration across physiographic gradients, including in current fire refugia, would also be helpful in establishing a foundation on which to base management decisions about fuels and fire across the landscape.

We also propose the establishment of restoration field trials focused on pine establishment, from seed and bare-root stock seedlings, under a range of manipulations,

including shading, seed predator protection, and water addition during the fore-summer dry season. Such experiments could elucidate the mechanisms responsible for recent pine recruitment failure, both in terms of environmental stresses and the stages of establishment that act as bottlenecks. These trials could also, of course, serve as pilots for actual restoration of pine species, to identify factors influencing successful tree recruitment and the feasibility of these efforts, as well establishing nuclei for future forest stands.

References

1. Barton AM. Intense wildfire in southeastern Arizona: transformation of a Madrean oak–pine forest to oak woodland. *Forest Ecol Manag.* 2002;165(1):205-12.
2. Savage M, Mast JN, Feddema JJ. Double whammy: high-severity fire and drought in ponderosa pine forests of the Southwest. *Canadian Journal of Forest Research.* 2013;43(6):570-83.
3. Taylor AH, Skinner CN. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. *Forest Ecol Manag.* 1998;111(2):285-301.
4. Camp A, Oliver C, Hessburg P, Everett R. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee Mountains. *Forest Ecol Manag.* 1997;95(1):63-77.
5. Kolden C, Bleeker T, Smith A, Poulos H, Camp A. Fire Effects on Historical Wildfire Refugia in Contemporary Wildfires. *Forests.* 2017;8. doi: 10.3390/f8100400.
6. Davis SD, Kolb KJ, Barton KP. Ecophysiological processes and demographic patterns in the structuring of California chaparral. In: Rundel PW, Montenegro G, Jaksic F, editors. *Landscape Disturbance and Biodiversity in Mediterranean-Type Ecosystems.* 136. Berlin: Springer Verlag; 1998. p. 297-310.
7. Kolb TW, Stone JE. Differences in leaf gas exchange and water relations among species and tree sizes in an Arizona pine–oak forest. *Tree Physiology* 2000;20:1-12.
8. Seager R, Ting M, Held I, Kushnir Y, Lu J, Vecchi G, et al. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science.* 2007;316(5828):1181-4.
9. Williams AP, Seager R, Berkelhammer M, Macalady AK, Crimmins MA, Swetnam TW, et al. Causes and implications of extreme atmospheric moisture demand during the record-breaking 2011 wildfire season in the southwestern United States. *Journal of Applied Meteorology and Climatology.* 2014;53(12):2671-84.
10. Swetnam TW, Baisan CH, editors. *Historical fire regime patterns in the southwestern United States since AD 1700. Fire Effects in Southwestern Forests, Proceedings of the 2nd La Mesa Fire Symposium; 1996 1994 March 29-31; Los Alamos, NM: USDA Forest Service; 1996.*
11. Swetnam TW, Baisan CH. Tree-ring reconstructions of fire and climate history in the Sierra Nevada and southwestern United States. In: Veblen TT, Baker W, Montenegro G, Swetnam TW, editors. *Fire and climatic change in temperate ecosystems of the western Americas. Ecological Studies.* 160: Springer; 2003. p. 158-95.
12. Westerling A, Brown T, Schoennagel T, Swetnam T, Turner M, Veblen T, editors. *Briefing: Climate and wildfire in western US forests. Forest conservation and management in the Anthropocene; 2014: USDA Forest Service; 2014.*
13. Leopold A. Grass, brush, timber, and fire in southern Arizona. *J Forest.* 1924;22(6):1-10.
14. Swetnam TW, Baisan CH, Kaib J. Forest fire histories of the sky islands of La Frontera. In: Webster GL, Bahre CJ, editors. *Changing plant life of La Frontera: observations on vegetation in the United States/Mexico borderlands* University of New Mexico Press, Albuquerque. Albuquerque, NM2001. p. 95-119.
15. Stephens SL, Ruth LW. Federal forest-fire policy in the United States. *Ecological Applications.* 2005;15(2):532-42.
16. Covington WW, Moore MM. Southwestern Ponderosa Forest Structure - Changes since Euro-American Settlement. *J Forest.* 1994;92(1):39-47. PubMed PMID: ISI:A1994MR05700014.
17. Allen CD, Savage M, Falk DA, Suckling KF, Swetnam TW, Schulke T, et al. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications.* 2002;12(5):1418-33.
18. Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW. Warming and earlier spring increase western

US forest wildfire activity. *Science*. 2006;313(5789):940-3.

19. Abatzoglou JT, Williams AP. Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences*. 2016;113(42):11770-5.
20. Keane RE, Holsinger LM, Parsons RA, Gray K. Climate change effects on historical range and variability of two large landscapes in western Montana, USA. *Forest Ecol Manag*. 2008;254(3):375-89.
21. Dennison PE, Brewer SC, Arnold JD, Moritz MA. Large wildfire trends in the western United States, 1984–2011. *Geophysical Research Letters*. 2014;41(8):2928-33.
22. Keane RE, Hessburg PF, Landres PB, Swanson FJ. The use of historical range and variability (HRV) in landscape management. *Forest Ecol Manag*. 2009;258(7):1025-37.
23. Strom BA, Fulé PZ. Pre-wildfire fuel treatments affect long-term ponderosa pine forest dynamics. *International Journal of Wildland Fire*. 2007;16:128-38.
24. Haire S, Mcgarigal K. Inhabitants of Landscape Scars: Succession of Woody Plants After Large, Severe Forest Fires in Arizona and New Mexico. *The Southwestern Naturalist*. 2008;53:146-61.
25. Shive KL, Sieg CH, Fulé PZ. Pre-wildfire management treatments interact with fire severity to have lasting effects on post-wildfire vegetation response. *Forest Ecology and Management*. 2013;297:75-83.
26. Coop J, Parks SA, McClernan S, Holsinger L. Influences of prior wildfires on vegetation response to subsequent fire in a reburned Southwestern landscape. *Ecological Applications*. 2016;26:346–54. doi: 10.1890/15-0775.
27. Savage M, Mast JN. How resilient are southwestern ponderosa pine forests after crown fires? *Canadian Journal of Forest Research*. 2005;35:967-77.
28. Beisner BE, Haydon DT, Cuddington K. Alternative stable states in ecology. *Front Ecol Environ*. 2003;1(7):376-82.
29. Falk DA, editor Are Madrean ecosystems approaching tipping points? Anticipating interactions of landscape disturbance and climate change. Merging science and management in a rapidly changing world: Biodiversity and management of the Madrean Archipelago III; 2013; Tucson, AZ: U.S. Department of Agriculture; 2013.
30. Moore MM, Wallace Covington W, Fulé PZ. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. *Ecological Applications*. 1999;9(4):1266-77.
31. Martinson EJ, Omi PN. Assessing mitigation of wildfire severity by fuel treatments an example from the Coastal Plain of Mississippi. *Int J Wildland Fire*. 2008;17(3):415-20. PubMed PMID: ISI:000256940100010.
32. Toledo VM, Ortiz B, Medellín S. Biodiversity islands in a sea of pasturelands: indigenous resource management in the humid tropics of Mexico. *Etnoecológica*. 1994;2(3):30-44.
33. Poulos HM, Taylor AH, Beaty RM. Environmental controls on dominance and diversity of woody plant species in a Madrean, Sky Island ecosystem, Arizona, USA. *Plant Ecology*. 2007;193(1):15-30.
34. Poulos HM, Camp AE. Topographic influences on vegetation mosaics and tree diversity in the Chihuahuan Desert Borderlands. *Ecology*. 2010;91(4):1140-51. PubMed PMID: ISI:000277525300021.
35. Coblenz DD, Riitters KH. Topographic controls on the regional-scale biodiversity of the southwestern USA. *Journal of Biogeography*. 2004;31(7):1125-38.
36. Fulé PZ, Covington W. Spatial patterns of Mexican pine-oak forests under different recent fire regimes. *Plant Ecology*. 1998;134(2):197-209.
37. Fulé P, Covington W. Changing fire regimes in Mexican pine forests: Ecological and management implications. *Journal of Forestry*. 1996;94:33-8.
38. Kaib JM, Baisan CH, Swetnam TW, editors. Fire history in the gallery pine-oak forests and adjacent grasslands of the Chiricahua Mountains, Arizona. *Effects of Fire on Madrean Province Ecosystems*; 1996; Tucson, AZ: USDA Forest Service; 1996.
39. Kaib JM. Fire history in riparian canyon pine-oak forests and the intervening desert grasslands of the southwest borderlands: A dendroecological, historical and cultural inquiry. Tucson, AZ: The University of Arizona; 1998.
40. Barton AM. Pines versus oaks: effects of fire on the composition of Madrean forests in Arizona. *Forest Ecol Manag*. 1999;120(1):143-56.
41. Rodríguez-Trejo DA, Fulé PZ. Fire ecology of Mexican pines and a fire management proposal. *Int J Wildland Fire*. 2003;12(1):23-37.

42. Baumgartner KH, Fulé PZ. Survival and sprouting responses of Chihuahua pine after the Rodeo-Chediski fire on the Mogollon Rim, Arizona. *Western North American Naturalist*. 2007;67(1):51-6.
43. DeBano LH, Ffolliott PH, Ortega-Rubio A, Gottfried GJ, Hamre RH, Carleton B, editors. Biodiversity and management of the madrean archipelago: the sky islands of southwestern United States and northwestern Mexico. Rocky Mountain Forest and Range Experiment Station, General Technical Report; 1995; Tucson, AZ: USDA Forest Service.
44. Drewes H, Williams F. Mineral resources of the Chiricahua Wilderness area. US Geological Survey; 1973.
45. Adams DK, Comrie AC. The North American Monsoon. *Bulletin of the American Meteorological Society*. 1997;78(10):2197-213.
46. Barton AM, Swetnam TW, Baisan CH. Arizona pine (*Pinus arizonica*) stand dynamics: local and regional factors in a fire-prone madrean gallery forest of Southeast Arizona, USA. *Landscape Ecology*. 2001;16(4):351-69.
47. Youberg A, Neary DG, Koestner KA, Koestner PE, editors. Post-wildfire erosion in the Chiricahua Mountains. Merging science and management in a rapidly changing world: Biodiversity and management of the Madrean Archipelago III; 2013 2012 May 1-5; Tucson, AZ: USDA Forest Service, Rocky Mountain Research Station.
48. Arechederra-Romero L. Southwest Fire Science Consortium Field Trip to the Chiricahua National Monument: Discussion of the Impacts of the 2011 Horseshoe 2 Fire. *Environmental Geology, Arizona Geology Magazine* [Internet]. 2012 15 April 2017. Available from: <http://azgeology.azgs.az.gov/article/environmental-geology/2012/12/southwest-fire-science-consortium-field-trip-chiricahua>.
49. Whittaker RH, Niering WA. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient. *Ecology*. 1975;56:771-90.
50. Felger RS, Wilson MF, editors. Northern Sierra Madre Occidental and its Apachian outliers: a neglected center of biodiversity. Biodiversity and management of the madrean archipelago: the sky islands of southwestern United States and northwestern Mexico; 1994; Tucson, AZ: USDA Forest Service; 1995.
51. Warshall P, editor The Madrean sky island archipelago: a planetary overview. Biodiversity and management of the Madrean Archipelago: the sky islands of southwestern United States and northwestern Mexico; 1995; Tucson, AZ: USDA Forest Service.
52. Danzer SR, Baisan CH, Swetnam TW, editors. The influence of fire and land-use history on stand dynamics in the Huachuca Mountains of Southeastern Arizona. *Effects of Fire on Madrean Province Ecosystems*; 1996; Tucson, AZ: USDA Forest Service; 1996.
53. Huebner CD, Vankat JL. The importance of environment vs. disturbance in the vegetation mosaic of Central Arizona. *J Veg Sci*. 2003;14(1):25-34.
54. Barton AM. Gradient analysis of relationships among fire, environment, and vegetation in a southwestern USA mountain range. *Bulletin of the Torrey Botanical Club*. 1994;121:251-65.
55. The PLANTS Database [Internet]. National Plant Data Team. 2017 [cited 12 June 2017]. Available from: <http://plants.usda.gov>.
56. Lawrimore JH, Menne MJ, Gleason BE, Williams CN, Wuertz DB, Vose RS, et al. An overview of the Global Historical Climatology Network monthly mean temperature data set, version 3. *J Geophys Res*. 2011;116:D19121. doi: 10.1029/2011JD016187.
57. USDA Forest Service Coronado National Forest GIS Data [Internet]. 2013 [cited 15 August 2017]. Available from: <http://www.fs.usda.gov/detail/r3/landmanagement/gis/?cid=stelprdb5208076>.
58. Pinheiro J, Bates D, DebRoy S, Sarkar D. R Core Team (2014) nlme: linear and nonlinear mixed effects models. R package version 3.1-117. Available at <http://CRAN.R-project.org/package=nlme>. 2014.
59. R Development Core Team. A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2017.
60. Barton AM. Factors controlling plant distributions: drought, competition, and fire in montane pines in Arizona. *Ecol Monogr*. 1993;63(4):367-97.
61. Parker AJ. The topographic relative moisture index: an approach to soil-moisture assessment in mountain terrain. *Physical Geography*. 1982;3(2):160-8.
62. ArcGIS E. Release 10.3 Environmental Systems Research Institute. Redlands, CA. 2014.

63. Holden ZA, Abatzoglou JT, Luce CH, Baggett LS. Empirical downscaling of daily minimum air temperature at very fine resolutions in complex terrain. *Agricultural and Forest Meteorology*. 2011;151(8):1066-73.
64. Miller JD, Thode AE. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). *Remote Sensing of Environment*. 2007;109(1):66-80.
65. Kolden CA, Smith AM, Abatzoglou JT. Limitations and utilisation of Monitoring Trends in Burn Severity products for assessing wildfire severity in the USA. *Int J Wildland Fire*. 2015;24(7):1023-8.
66. Buuren S, Groothuis-Oudshoorn K. mice: Multivariate imputation by chained equations in R. *Journal of Statistical Software*. 2011;45(3):1-67. doi: 10.18637/jss.v045.i03.
67. McCune B, Mefford MJ. PC-ORD. Multivariate Analysis of Ecological Data. MJM Software Designs; 2011.
68. Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, et al. Modeling Zero-Inflated Count Data With glmmTMB. *bioRxiv*. 2017:132753.
69. Barton AM, Teeri JA. The ecology of elevational positions in plants: drought resistance in five montane pine species in southeastern Arizona. *Am J Bot*. 1993;15-25.
70. English NB, McDowell NG, Allen CD, Mora C. The effects of α -cellulose extraction and blue-stain fungus on retrospective studies of carbon and oxygen isotope variation in live and dead trees. *Rapid Communications in Mass Spectrometry*. 2011;25(20):3083-90.
71. Farquhar GD, Sharkey TD. Stomatal conductance and photosynthesis. *Annual review of plant physiology*. 1982;33(1):317-45.
72. McCarroll D, Loader NJ. Stable isotopes in tree rings. *Quaternary Science Reviews*. 2004;23(7):771-801.
73. O'Leary MH. Carbon isotope fractionation in plants. *Phytochemistry*. 1981;20(4):553-67.
74. Farquhar G, Richards R. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Functional Plant Biology*. 1984;11(6):539-52.
75. Cocke AE, Fule PZ, Crouse JE. Forest change on a steep mountain gradient after extended fire exclusion: San Francisco Peaks, Arizona, USA. *Journal of Applied Ecology*. 2005;42(5):814-23.
76. Young D, Latimer A. Post-fire forest regeneration in a changing climate. Joint Fire Sciences Program Report. 2017 September 2017. Report No.: 15-2-01-34.
77. Bond WJ, Midgley JJ. Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol Evol*. 2001;16(1):45-51.
78. Frazer J, Davis S. Differential survival of chaparral seedlings during the first summer drought after wildfire. *Oecologia*. 1988;76(2):215-21.
79. Haire SL, McGarigal K. Effects of Landscape Patterns of Fire Severity on Regenerating Ponderosa Pine Forests (*Pinus ponderosa*) in New Mexico and Arizona, USA. *Landscape Ecology*. 2010;25:1055-69.
80. Haffey CM. Patterns and predictors of crown fire induced type conversion in dry conifer forests. Flagstaff, AZ: Northern Arizona University; 2014.
81. Collins BM, Roller GB. Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. *Landscape Ecology*. 2013;28(9):1801-13.
82. Iniguez JM, Swetnam TW, Baisan CH. Spatially and temporally variable fire regime on Rincon Peak, Arizona, USA. *Fire Ecology Special Issue*. 2009;5:3-21.
83. Minor J, Falk D, Barron-Gafford G. Fire Severity and Regeneration Strategy Influence Shrub Patch Size and Structure Following Disturbance. *Forests*. 2017;8:221. doi: 10.3390/f8070221.
84. Fulé P. Effects of an intense wildfire in a Mexican oak-pine forest. *Forest Science*. 2000;46(1):52-61.
85. Clarke PJ. Habitat islands in fire-prone vegetation: Do landscape features influence community composition? *Journal of Biogeography*. 2002;29(5-6):677-84.
86. Krawchuk MA, Haire SL, Coop J, Parisien MA, Whitman E, Chong G, et al. Topographic and fire weather controls of fire refugia in forested ecosystems of northwestern North America. *Ecosphere*. 2016;7(12). doi: 10.1002/ecs2.1632.
87. Schwilk DW, Keeley JE. The role of fire refugia in the distribution of *Pinus sabiniana* (Pinaceae) in the southern Sierra Nevada. *Madrone*. 2006;53(4):364-72.
88. Tardieu F, Simonneau T. Variability among species of stomatal control under fluctuating soil water

- status and evaporative demand: modelling isohydric and anisohydric behaviours. *J Exp Bot.* 1998;419-32.
89. Tardieu F. Will increases in our understanding of soil-root relations and root signalling substantially alter water flux models? *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences.* 1993;341(1295):57-66. doi: 10.1098/rstb.1993.0091.
 90. Breshears DD, Myers OB, Meyer CW, Barnes FJ, Zou CB, Allen CD, et al. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Front Ecol Environ.* 2009;7(4):185-9. PubMed PMID: ISI:000265971200017.
 91. McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, et al. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* 2008;178(4):719-39. PubMed PMID: ISI:000255722300005.
 92. Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, Balice RG, et al. Regional vegetation die-off in response to global-change-type drought. *P Natl Acad Sci USA.* 2005;102(42):15144-8. doi: DOI 10.1073/pnas.0505734102. PubMed PMID: ISI:000232811800038.
 93. Allen CD, Breshears DD. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proc Natl Acad Sci U S A.* 1998;95(25):14839-42. Epub 1998/12/09. PubMed PMID: 9843976; PubMed Central PMCID: PMC24536.
 94. Cooper CE, Muir JP, Morgan CL, Moore GW. Tortoise or hare: Will resprouting oaks or reseeding pines dominate following severe wildfire? *Forest Ecol Manag.* 2018;408:54-66.
 95. Clemente AS, Rego FC, Correia OA. Growth, water relations and photosynthesis of seedlings and resprouts after fire. *Acta Oecologica.* 2005;27(3):233-43.
 96. Martínez-Sancho E, Dorado-Liñán I, Gutiérrez Merino E, Matiu M, Helle G, Heinrich I, et al. Increased water-use efficiency translates into contrasting growth patterns of Scots pine and sessile oak at their southern distribution limits. *Global change biology.* 2017.
 97. Martin-Benito D, Anchukaitis JK, Evans NM, del Río M, Beeckman H, Cañellas I. Effects of Drought on Xylem Anatomy and Water-Use Efficiency of Two Co-Occurring Pine Species. *Forests.* 2017;8(9). doi: 10.3390/f8090332.
 98. Richardson AD, Berlyn GP. Spectral reflectance and photosynthetic properties of *Betula papyrifera* (Betulaceae) leaves along an elevational gradient on Mt. Mansfield, Vermont, USA. *Am J Bot.* 2002;89(1):88-94.
 99. Sims DA, Gamon JA. Relationships between leaf pigment content and spectral reflectance across a wide range of species, leaf structures and developmental stages. *Remote sensing of environment.* 2002;81(2):337-54.
 100. Poulos HM, Goodale UM, Berlyn GP. Drought response of two Mexican oak species, *Quercus laceyi* and *Q. sideroxyla* (Fagaceae), in relation to elevational position. *Am J Bot.* 2007;94(5):809-18. PubMed PMID: ISI:000249830400012.
 101. Carter GA. Responses of Leaf Spectral Reflectance to Plant Stress. *Am J Bot.* 1993;80(3):239-43. doi: 10.2307/2445346.
 102. Carter GA, Knapp AK. Leaf optical properties in higher plants: linking spectral characteristics to stress and chlorophyll concentration. *Am J Bot.* 2001;88(4):677-84.
 103. Silvertown J, Gordon DM. A framework for plant behavior. *Annual Review of Ecology and Systematics.* 1989;20(1):349-66.
 104. Sultan S, Bazzaz F. Phenotypic plasticity in *Polygonum persicaria*. I. Diversity and uniformity in genotypic norms of reaction to light. *Evolution.* 1993;47(4):1009-31.
 105. Callaway RM, Pennings SC, Richards CL. Phenotypic plasticity and interactions among plants. *Ecology.* 2003;84(5):1115-28.
 106. Poulos H, Goodale U, Berlyn G. Drought response of two Mexican oak species, *Quercus laceyi* and *Q. sideroxyla* (Fagaceae), in relation to elevational position. *Am J Bot.* 2007;94(5):809-18.
 107. Poulos HM. A Review of the Evidence for Pine-Oak Niche Differentiation in the American Southwest. *Journal of Sustainable Forestry.* 2009;28(1).
 108. Poulos HM, Berlyn GP. Variability in needle morphology and water status of *Pinus cembroides* across an elevational gradient in the Davis Mountains of west Texas, USA. *J Torrey Bot Soc.* 2007;134(2):281-8. PubMed PMID: ISI:000248354400011.
 109. Gratani L. Plant phenotypic plasticity in response to environmental factors. *Advances in botany.*

2014;2014.

110. Schwilk DW, Brown TE, Lackey R, Willms J. Post-fire resprouting oaks (genus: *Quercus* exhibit plasticity

in xylem vulnerability to drought. *Plant ecology*. 2016;217(6):697-710.

111. Hodgkinson KC. Water relations and growth of shrubs before and after fire in a semi-arid woodland. *Oecologia*. 1992;90(4):467-73.

112. Richards MB, Lamont BB. Post-fire mortality and water relations of three congeneric shrub species under extreme water stress—a trade-off with fecundity? *Oecologia*. 1996;107(1):53-60.

113. Abatzoglou JT, Kolden CA. Relationships between climate and macroscale area burned in the western United States. *Int J Wildland Fire*. 2013;22(7):1003-20.

114. van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fule PZ, et al. Widespread Increase of Tree Mortality Rates in the Western United States. *Science*. 2009;323(5913):521-4. doi: DOI 10.1126/science.1165000. PubMed PMID: ISI:000262587900047.

115. Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, et al. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecol Manag*. 2010;259(4):660-84. doi: DOI 10.1016/j.foreco.2009.09.001. PubMed PMID: ISI:000275014400002.

116. Enright N, Fontaine J, Bowman D, Bradstock R, Williams R. Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment*. 2015;13:265-72. doi: 10.1890/140231.

117. Adams MA. Mega-fires, tipping points and ecosystem services: Managing forests and woodlands in an uncertain future. *Forest Ecol Manag*. 2013;294:250-61.

118. Petrie M, Wildeman A, Bradford JB, Hubbard R, Lauenroth W. A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. *Forest Ecol Manag*. 2016;361:328-38.

119. Brown PM, Wu R. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology*. 2005;86(11):3030-8.

120. Guiterman C, Margolis E, Allen C, Falk D, Swetnam T. Long-term persistence and fire resilience of oak shrubfields in dry conifer forests of northern New Mexico. *Ecosystems*. 2017. doi: 10.1007/s10021-017-0192-2.

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Appendix B: List of Completed/Planned Scientific/Technical Publications/Science Delivery Products

The following products were completed during the course of the project:

- Manuscript submitted to peer-reviewed academic journal (*Forest Ecology and Management*)
- Manuscript submitted to peer-reviewed academic journal (*Journal of Ecology*)
- Conference presentation (Barton and Poulos): Association for Fire Ecology, Annual Conference, Tucson, AZ, December 2016, Title: Post-fire forest regeneration under climate change
- Conference presentation (Poulos, Barton, Berlyn): Association for Fire Ecology, Annual Conference, Tucson, AZ, December 2016, Title: Post-fire forest regeneration under climate change
- Conference presentation (Barton and Poulos): Association for Fire Ecology, Annual Conference, Orlando, FL, December 2017, Title: Post-fire forest regeneration under climate change
- Invited Presentation (Barton): American Museum of Natural History, Southwestern Research Station, June 2016, Title:
- Invited Presentation (Poulos and Barton): Yale University, School of Forestry & Environmental Studies, March 2017, Title:
- Field Tour (Barton and Poulos) for land management agencies, researchers, community members. June 2016. Cave Creek Canyon, Chiricahua Mountains, Coronado National Forest. Two-hour tour and discussion about the project, the Horseshoe Two Fire, and collaboration among land management agencies, scientists, and community members.

The following products are planned for after the completion of the project:

- Manuscript to be submitted by April 2018 to peer-reviewed academic journal
- Webinar (Poulos and Barton), Southwest Fire Consortium, 2018
- Conference presentation (Barton and Poulos): Madrean Conference: Collaboration now for the future: biodiversity and management of the Madrean Archipelago VI, Tucson, AZ, May 14-18, 2018

Appendix C: Metadata

This project generated a large amount of new data from field sampling and the generation of raster and remotely-sensed information. The stand structure data set (structure.csv) includes all non-physiological data collected at each of the 68 plots: plot number; plot physiography; field-collected environmental variables; derived raster environmental variables; which of the two fires burned at the location; dNBR for the Horseshoe Two Fire; field-determined fire-severity; cover for all woody species; number of seedlings and resprouts of pine by species; for each pine species the distance to the nearest seed tree; the number of seedlings and resprout genets of oaks by species. The physiology data set (physiology.csv) includes the following for plots in which these parameters were measured: plot number; plot physiography; field-collected environmental variables; derived raster environmental variables; which of the two fires burned at the location; dNBR for the Horseshoe Two Fire; field-determined fire-severity, and the following variables for each tree species: maximum photosynthetic rate, stomatal conductance, transpiration, instantaneous water use efficiency, leaf spectral reflectance, leaf chlorophyll and anthocyanin content, relative water content, and leaf mass per unit area.

Each of the two datasets is accompanied by metadata following the “FGDC Biological Data Profile” standard of the Content Standard for Digital Geospatial Data (FGDC-STD-001.1-1999). The data and accompanying metadata will be archived in the JFSP-recommended repository, the Forest Service Research Data Archive, upon publication of a peer-reviewed paper presenting the data

Appendix D: Detailed Statistical Results for Recruitment vs. dNBR

Hurdle regression results for the effects of fire-severity (dNBR in the 2011 Horseshoe Two Fire), TRMI (topographic relative moisture index), elevation, solar radiation, and landscape dissection on the density of seedlings and resprouts for pines and oaks. Statistical significance: ^{ns} $P > 0.05$;

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. $N = 67$ plots.

Variable	Estimate	Std. Err.	z value	Pr(> z)	Model	Significance
<u><i>P. engelmannii</i> seedlings</u>						
dNBR	-0.0028	0.001025	-2.73	0.00633	binomial	**
TRMI	0.09276	0.03603	2.575	0.01003	binomial	*
elevation	0.2565	0.6141	0.418	0.676	binomial	ns
radiation	-19.57	60.25	-0.325	0.745	binomial	ns
dissection	-0.4783	0.2567	-1.863	0.0625	binomial	ns
<u><i>P. leiophylla</i> seedlings</u>						
dNBR	-0.003507	0.001038	-3.377	0.000733	binomial	***
TRMI	0.06645	0.03171	2.096	0.0361	binomial	*
elevation	-0.37636	0.25968	-1.449	0.147	binomial	ns
radiation	0.1795	0.2478	0.724	0.469	binomial	ns
dissection	0.2334	0.223	1.047	0.295	binomial	ns
<u><i>P. leiophylla</i> resprouts</u>						
dNBR	-0.0009779	0.0005538	-1.766	0.0774	binomial	ns
TRMI	0.04775	0.01248	3.825	0.000131	neg binomial	***
elevation	-0.6518	0.1747	-3.732	0.00019	binomial	***
radiation	0.04846	0.17374	0.279	0.78	binomial	ns
dissection	-0.1968	0.1127	-1.746	0.080774	binomial	ns
<u><i>Q. hypoleucoides</i> seedlings</u>						
dNBR	-0.00303	0.001016	-2.984	0.00285	binomial	**
TRMI	0.001118	0.036848	0.03	0.9758	binomial	ns
elevation	0.1237	0.3455	0.358	0.7203	binomial	ns
radiation	0.814	0.5007	1.626	0.104	binomial	ns
dissection	0.217	0.4259	0.509	0.6104	binomial	ns
<u><i>Q. hypoleucoides</i> resprouts</u>						
dNBR	0.0020568	0.0002805	7.333	2.25E-13	neg binomial	***
TRMI	-0.055377	0.009588	-5.776	7.66E-09	neg binomial	***
elevation	0.56667	0.11044	5.131	2.88E-07	neg binomial	***
radiation	-0.1382	0.1144	-1.208	0.22695	neg binomial	ns
dissection	0.19608	0.09131	2.147	0.03176	neg binomial	*
<u><i>Q. arizonica</i> seedlings</u>						
dNBR	-0.003508	0.001033	-3.395	0.000687	neg binomial	***
TRMI	0.11486	0.03705	3.1	0.00193	neg binomial	**
elevation	-0.76882	0.301	-2.554	0.0106	neg binomial	*
radiation	0.21079	0.2496	0.845	0.398	neg binomial	ns
dissection	-0.2773	0.2254	-1.23	0.219	neg binomial	ns

O. arizonica resprouts

dNBR	0.001187	0.0003051	3.89	1.00E-04	neg binomial	***
TRMI	-0.04454	0.00958	-4.649	3.34E-06	neg binomial	***
elevation	0.41574	0.10548	3.942	8.10E-05	neg binomial	***
radiation	0.0006461	0.0003821	1.691	0.09089	neg binomial	ns
dissection	0.17885	0.08894	2.011	0.044327	neg binomial	*

O. emoryi seedlings

dNBR	-0.006478	2.02E-03	-3.207	0.00134	binomial	**
TRMI	0.13471	0.04755	2.833	0.004613	binomial	**
elevation	-1.373	0.4347	-3.159	0.00158	binomial	**
radiation	0.41	0.3553	1.154	0.248	binomial	ns
dissection	-0.42531	0.29689	-1.433	0.152	binomial	ns

O. emoryi resprouts

dNBR	-0.005114	0.001522	-3.361	0.000777	binomial	***
TRMI	0.01825	0.02617	0.697	0.486	binomial	ns
elevation	-0.09188	0.25295	-0.363	0.716	binomial	ns
radiation	-0.1474	0.1892	-0.779	0.436	binomial	ns
dissection	-0.1991	0.1765	-1.128	0.259285	binomial	ns